Speciation

The realization that the Red Queen and Court Jester models may be scale-dependent, and that evolution may be pluralistic (*3*), opens opportunities for dialog. Taxic studies in paleontology continue to have great value in highlighting correlations between species richness and other factors, but comparative phylogenetic methods will illuminate questions about clade dynamics, species richness, and the origin of novelties. Further, methods are shared by paleontologists and neontologists, and this allows direct communication on the patterns and processes of macroevolution. Viewed close up, evolution is all about biotic interactions in ecosystems (Red Queen model), but from further away, the large patterns of biodiversity are driven by the physical environment (Court Jester model).

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REVIEW

Adaptive Radiation: Contrasting Theory with Data

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Biologists have long been fascinated by the exceptionally high diversity displayed by some evolutionary groups. Adaptive radiation in such clades is not only spectacular, but is also an extremely complex process influenced by a variety of ecological, genetic, and developmental factors and strongly dependent on historical contingencies. Using modeling approaches, we identify 10 general patterns concerning the temporal, spatial, and genetic/morphological properties of adaptive radiation. Some of these are strongly supported by empirical work, whereas for others, empirical support is more tentative. In almost all cases, more data are needed. Future progress in our understanding of adaptive radiation will be most successful if theoretical and empirical approaches are integrated, as has happened in other areas of evolutionary biology.

The spectacular diversity of life on Earth that Darwin sought to explain in *On the Origin of Species* emerged through a variety of intricate biological processes. One of these is adaptive radiation, which some consider of foremost importance and potentially responsible for much of the ecological and phenotypic diversity of life (*1, 2*). "Adaptive radiation" refers to those evolutionary groups that have exhibited an exceptional extent of adaptive diversification into a variety of ecological niches (*2–4*), with such divergence often occurring extremely rapidly (*5*). Classic examples of adaptive radiation include Darwin's finches on the Galápagos islands, *Anolis* lizards on Caribbean islands (Fig. 1), Hawaiian silverswords, and cichlids of the East African Great Lakes (Fig. 2), among many others (*1, 2, 6*).

Adaptive radiation has two components: the production of new species (speciation) and the adaptation of constituent species to a diversity of ecological niches. Although many classic adaptive radiations are both species rich and adaptively disparate (*7*), this correlation is far from perfect: Some adaptive radiations have relatively low species richness (e.g., Darwin's finches, Australian pygopodid lizards); alternatively, some speciose clades contain little adaptive disparity and thus would not qualify as adaptive radiations (*3, 8*).

The classic view of adaptive radiation focuses on ecological opportunity, in which an ancestral species finds itself in an environment in which resources are abundant and underutilized. Such resource availability may result from coloniza-tion of an underpopulated area (e. g., island or lake), extinction of previously ecologically dominant groups, or evolution of a character—sometimes termed a "key innovation"—that allows the lineage to interact with the environment in novel ways (*1, 2*). Different evolutionary factors allowing the populations to take advantage of new ecological opportunity have been emphasized, including genetic drift in small founder or peripheral populations (*9*), relaxed (*9*) or strong selection (*2, 10*), and hybridization (*11, 12*).

Empirical Approaches for Studying Adaptive Radiation

Four main empirical approaches have been used:

Fossils. Methods based on fossil data allow one to infer the history of the clade through time and to use information from extinct taxa. The disadvantages of this approach are incompleteness of the fossil record, difficulty in assessing the adaptive significance of phenotypic variation among taxa, and the absence of ecological, behavioral, physiological, and other types of data.

Phylogenetic comparative methods. Phylogenetic approaches take advantage of increasingly complete phylogenies for many important groups and have the ability to integrate studies of the evolution of organismal function and ecology. The main disadvantage of these methods is that extinct taxa are often not represented so that there is no way, for example, to detect whether a clade has been more species-rich in the past. Moreover, phylogenetic inferences about character states in the past can be unreliable (*13, 14*).

Microevolutionary studies of extant taxa. Studies focusing on traits of and processes affecting extant taxa—e.g., phenotypic characters, ecological niches, spatial structure, genetics, local adaptation, competition, and sexual selection—can elucidate much about the processes driving

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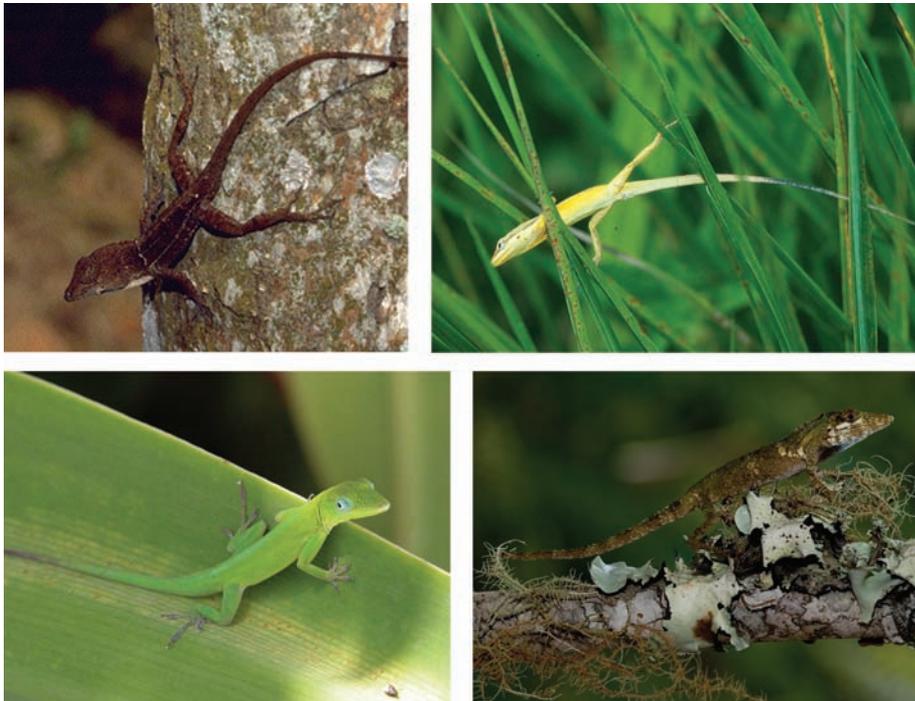
Fig. 1. Adaptive diversification in Caribbean *Anolis* lizards. On each island in the Greater Antilles, anoles have diversified to produce the same set of habitat specialists. Shown here (clockwise from top left) are *A. cybotes*, trunk-ground specialist, Hispaniola (photo: J. Losos); *A. pulchellus*, grass-bush, Puerto Rico (photo: J. Losos); *A. insolitus*, twig, Hispaniola (photo: L. Mahler); *A. chlorocyanus*, trunk-crown, Hispaniola (photo: M. Losos).

adaptive radiation and sometimes even include manipulative experiments. However, extrapolation from processes operating today to what happened early in the history of a radiation is problematic; in the past, different processes may have operated or the outcome of these processes may have been different. These differences might result because conditions may have been different early in a radiation's history, including greater resource abundance, less ecological specialization, and less genetic canalization. Alternatively, one can study taxa that may be in early stages of radiation (e.g., stickleback fishes), but such ecologically and morphologically nondisparate groups are not necessarily good models for the early stages of adaptive radiation.

Adaptive radiation in the laboratory. The advantage of studies of adaptive radiation in microbial microcosms [e.g., (*15*, *16*)] and digital cyberworlds (*17*) is experimental flexibility. However, it is not clear whether these systems are good analogs to adaptive radiations in nature.

Mathematical Modeling

Adaptive radiation can also be studied by using mathematical methods. The latter have traditionally played a major role both in evolutionary biology and in ecology. For example, the modern synthesis of the 1930s and 1940s was a direct result of the development of theoretical population genetics by Fisher, Wright, and Haldane (*18*). A quantitative theory of speciation, which

has emerged over the past 40 years [reviewed in (*19–21*)], has clarified many questions and topics hotly debated by generations of biologists. The main advantages of mathematical modeling are its generality, the ability to identify crucial parameters, factors, and relevant temporal and spatial scales, as well as to point to the gaps in biological knowledge and intuition. However, the biological realism of models and their underlying assumptions can always be questioned.

Our goal here is threefold. First, we summarize recent theoretical findings on the dynamics of adaptive radiation. Second, we attempt to test theoretical predictions against existing data obtained using a variety of empirical approaches. Third, we identify important areas of theoretical and empirical research where notable advances can soon occur and can contribute dramatically to improving our understanding of adaptive radiation and the generation of biodiversity.

Dynamic Models of Adaptive Radiation—Extensions on Speciation Theory

Adaptive radiation can be viewed as the processes of speciation and adaptation extended to larger spatial and temporal scales. In classifying mechanisms of speciation (and, by extension, adaptive radiation), different approaches are possible. Most commonly, mechanisms of speciation are discussed according to the level of migration between the diverging (sub)populations (*9*, *22*). In this classification, the basic modes of specia-

tion are allopatric, parapatric, and sympatric, corresponding to zero, intermediate, and maximum migration, respectively (*19–21*). Alternatively, mechanisms of speciation can be classified according to biological mechanisms driving divergence and speciation, e.g., random drift, ecological selection, or sexual selection (*23*, *24*).

However, sometimes very different biological mechanisms have underlying dynamic commonalities and therefore can be described by very similar mathematical models. Therefore, classifying mechanisms of speciation and adaptive radiation on the basis of similarity of the corresponding models can be more general and insightful than on the basis of particular biological factors.

Five partially overlapping sets of models can be identified. In "spontaneous clusterization" models, an initially random mating population accumulates a substantial amount of genetic variation by mutation, recombination, and random drift and then splits into partially or completely reproductively isolated groups [reviewed in (*20*)]. Spontaneous clusterization models describe the accumulation of Dobzhansky-Muller genetic incompatibilities, speciation by hybridization, divergence in mating preferences, or allochronic speciation (i.e., speciation via divergence in the timing of life-cycle events related to reproduction). In "invasion of empty niches" models [e.g., (*25*, *26*)], a few founders enter a new environment with a number of novel discrete ecological niches. As selection acts on the new genetic variation supplied by mutation, different lineages become adapted to and simultaneously develop genetic preferences for different ecological niches. Ecological and phenotypic diversification is accompanied by the growth in the densities of emerging species (Fig. 3). The process of local adaptation is opposed by deleterious gene flow from subpopulations adapting to alternative niches. Under these conditions, a reinforcement-like process can result in the evolution of premating reproductive isolation between different locally adapted groups. "Selection gradient" models [e.g., (*27*, *28*)] are similar to "invasion of empty niches" models except that environmental conditions vary in a continuous gradient-like fashion and selection for local adaptation acts on a single quantitative trait, the optimum value of which changes linearly across space. In "sympatric diversification" models [e.g., (*29*, *30*)], a spatial component is not present, so that these models describe sympatric speciation. In these models, emerging species specialize on relatively narrow parts of a continuous unimodal distribution of abundances of a particular set of resources. In the fifth set of models, diversification is driven by coevolutionary interactions [e.g., (*31*)].

Ten Patterns of Adaptive Radiation

In mathematical modeling, details do matter and generalizations are often difficult to make. But some general patterns do emerge in models of speciation and adaptive radiation. Here we re-

view and evaluate with empirical data 10 patterns concerning temporal, spatial, and genetic/morphological properties of adaptive radiation. In some cases, mathematical models and generalizations from data have suggested the same patterns independently.

1) Early burst of evolutionary divergence: Typically, there is a burst of speciation and morphological diversification soon after the beginning of the radiation rather than similar rates through time.

Mathematical models of adaptive radiation that explicitly describe microevolutionary processes predict a burst of speciation soon after colonization (25, 26). This happens because the rate of speciation declines as fewer niches remain empty (reduced ecological opportunity) and species become more specialized (increased genetic constraints). In addition, phenomenological null models of clade diversification (32, 33) predict that morphological disparity grows more rapidly than species diversity early in the clade history due to the structure of multidimensional phenotype space and contrasting effects of speciation and extinction on disparity and diversity.

Both paleontological and phylogenetic comparative data indicate that ecologically important morphological variation often arises early in a clade's history. The radiation of placental mammals is a classic example, with most modern orders appearing in the fossil record within a short period (34). Many fossil groups experience a peak in morphological disparity relatively early in their history and subsequently decline (35). Phylogenetic studies also indicate that major ecological differences often evolve early in clade history, such as tree versus ground Darwin's finches or the "ecomorph" habitat specialists of *Anolis* (12, 36).

An increasingly common theme in molecular studies of speciation is the finding of a burst of species diversification early in a clade's history (37, 38). This pattern is also seen in the fossil records for some groups. This finding is often discussed in the context of adaptive radiation as evidence for the early burst model of diversification. However, implicit in this discussion is the assumption that species diversity is correlated with adaptive diversity, an assumption that probably is often, but not always, correct. Coupling of studies of species diversification and the evolution of adaptive disparity is an important new direction (39).

2) Overshooting: An early increase in species diversity is followed by a decline that plateaus (or substantially decelerates).

Overshooting can result if speciation rate is decreasing and/or extinction rate is increasing in time. The rate of speciation can decrease because fewer niches remain empty (reduced ecological opportunity) and species become more specialized (increased genetic constraints). Mathematical models provide only partial support because overshooting is predicted only under some conditions (25).

There are several ways to examine these ideas. The most direct is to follow a radiation through history. Some clades do, in fact, exhibit an early peak in species richness, followed by a decline and then leveling-off of diversity (40); however, alternative interpretations exist to explain these patterns (41).

An alternative approach is to compare related clades of different ages, with the assumption that all else is equal [but see (42)]. Taking this approach, overshooting has also been demonstrated in a comparison of the *Tetragnatha* spiders of the Hawaiian islands, in which the relatively young (but not youngest) island of Maui has the most species; the high diversity is attained by having several niches occupied by sets of allopatric species. Gillespie (43) hypothesized that in time, the ranges of such species expand and come into contact, at which point competitive exclusion occurs, leading to a decrease in species richness on older islands. Among African Rift lakes, the dependence of cichlid species diversity on time, once corrected for lake surface area, appears to be L-shaped [figure 2d in (38)], as expected under overshooting.

3) Stages of radiation: All else being equal, the following sequence of the diversification events is expected: (i) divergence with respect to macrohabitat; (ii) evolution of microhabitat choice and divergence with respect to microhabitat; (iii) divergence with respect to traits that simultaneously control the degree of local adaptation and nonrandom mating; and (iv) divergence with respect to other traits controlling survival and reproduction.

This hypothesis is mostly based on generalizations from the mathematical theory of speci-

Fig. 2. Adaptive diversification in cichlids. Several examples of cichlids that use different habitats. (Upper left) *Gnathochromis permaxillaris* occurs in the deeper (>35 m) intermediate (rock-sand interface) habitat with sediment-rich bottoms in Lake Tanganyika. (Upper right) *Lethrinops furcifer* is found in sandy environments near beaches in Lake Malawi. (Center) *Hemitilapia oxyrhynchus*, which is found in shallow vegetated habitats in Lake Malawi. (Lower left) *Cyprichromis* sp. "Leptosoma Jumbo" (Nkondwe) occurs in open water in Lake Tanganyika. (Lower right) *Petrotilapia nigra* occurs in the upper part (>10 m) of the sediment-free rocky habitat of Lake Malawi. [Photographs by A. Konings]

ation (20). Only a limited amount of theoretical work has so far been done with models describing the evolution of various types of traits for a sufficiently long time. But in these cases, simulations did support the above hypothesis (25, 26). However, many factors can interfere with the order in which niche axes are partitioned during species divergence, such as strength of selection, available genetic variation, extent of environmental heterogeneity, or historical contingencies such as the ancestral starting condition of a clade (2, 20).

Stages hypotheses have been proposed for mountain New Guinea birds (divergence in habitat elevation first, followed by segregation in diet, foraging techniques, and size), *Phylloscopus* leaf warblers (order of divergence: body size, foraging morphology and behavior, habitat), cichlids and parrotfish (habitat, diet, sexually selected traits), and *Anolis* lizards (body size, structural microhabitat, microclimate) [reviewed in (44, 45)]. However, these hypotheses have been proposed on the basis of phylogenetic analyses that may be incapable of accurately identifying character states during early stages of a radiation for traits that are evolutionarily labile (45).

4) Area effects: Speciation driven by ecological factors is promoted by larger geographic areas (e.g., of islands or lakes).

Both mathematical models (20, 25) and verbal theory show that several factors might contribute to increasing speciation rates with area. First, larger areas imply that larger population sizes can be achieved, leading to increased selection efficiency and more advantageous mutations for selection to act upon. Second, the environment may be more heterogeneous in larger areas, thus containing more ecological niches. For example, a metric of niche availability better explains the extent of species diversity in Galápagos snails than does island area (46). Third, larger areas may allow for more opportunity for allopatric or parapatric speciation (25, 47). In all three cases in which this hypothesis has been examined (Caribbean *Anolis* lizards, Galápagos snails, and African cichlids), the area effect results in part because a threshold island/ lake area exists below which in situ cladogenesis does not occur, even though some islands below the threshold are environmentally quite heterogeneous (38, 46, 48).

5) Nonallopatric diversification: Speciation during adaptive radiation can occur in the absence of allopatry.

In the traditional view [e.g., (9, 49)], divergent adaptive evolution occurred in allopatric populations that adapted to different ecological niches and thus incidentally evolved reproductive isolation. Subsequent sympatry could lead to reinforcement of incomplete reproductive isolation and enhancement of ecological differences (character displacement).

Recent years have seen a resurgence of interest in nonallopatric modes of speciation driven by divergent natural selection pressures (19, 20, 50). In line with these theories, some see adaptive radiation as the expected outcome of sympatric or parapatric speciation in the context of abundant ecological opportunity. Mathematical models have identified a number of conditions promoting non-

Fig. 3. An illustration of an adaptive radiation in a mathematical model (25, 26). Each square represents a unit spatial area (patch). The color of the square defines the ecological niche assigned to the patch. Each local population is represented by a circle. The radius of the circle is proportional to the population size. The color of the circle defines the niche preferred by most individuals. Matching of the color of the corresponding square and circle (observed in most cases) means that most individuals in the patch prefer the ecological conditions they experience. In the case shown, there are eight different groups of species utilizing eight different ecological niches. Each of these groups is composed of two or three different species differentiated by mating preferences.

allopatric speciation, including strong disruptive selection, strong nonrandom mating, high levels of genetic variation, close correlation of traits experiencing disruptive selection with those controlling nonrandom mating, and absence of costs of being choosy in mating (19, 50). How common these conditions are in nature is controversial (20, 21).

The strongest evidence for nonallopatric adaptive radiation comes from examples of diversifica-

tion in areas in which it is hard to envision an allopatric phase. The classic case is the clade of 11 cichlid species found in a small and environmentally homogeneous crater lake in Cameroon (51). At the same time, the lack of speciation in some groups on relatively large and environmentally heterogeneous, but isolated, islands suggests that geographic isolation may be needed for speciation to occur, as discussed above.
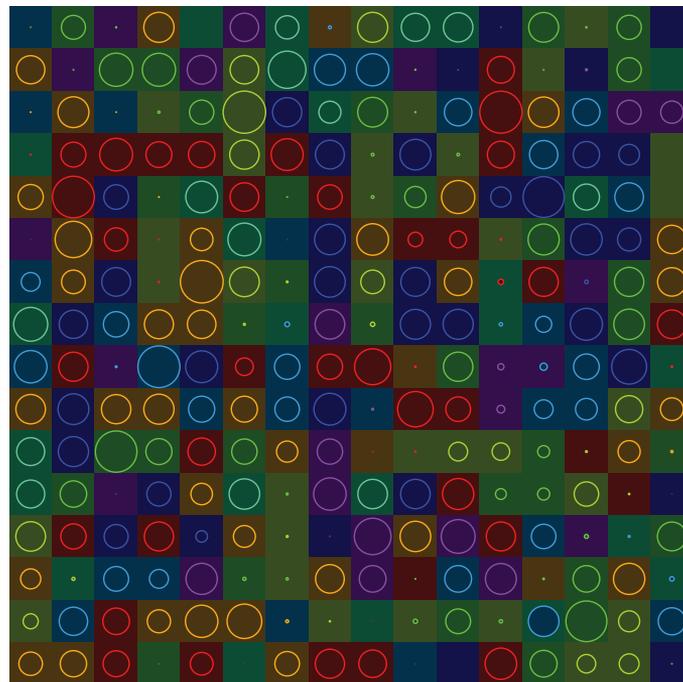
6) Selection gradient effect: Selection gradients of intermediate slopes promote speciation.

Models of parapatric speciation in which spatially heterogeneous selection for local adaptation acts on an additive trait (27, 28) show that if selection gradients are too shallow, differences in selection experienced in different parts of the species range are not strong enough to drive divergence and speciation. If selection gradients are too steep, selection is so strong that it prevents the population's spread into unoccupied areas with different selection. As a result, intermediate slopes of selection gradients are most conducive for speciation. This prediction is supported by a recent study of divergence in male coloration and female preferences in cichlids (52).

7) Spatial dimensionality effect: All else being equal, geographic areas that can approximately be viewed as one-dimensional (such as rivers or shores of lakes and oceans) promote more speciation and tend to maintain higher species richness and phenotypic and genetic diversity per unit area than geographic areas that are two-dimensional (such as lakes, oceans, and continental areas).

This prediction follows both from classical results on patterns of geographic variation in neutral loci induced by isolation by distance [e.g., (53)] and from speciation models (20). This spatial dimensionality effect may have contributed to the extraordinary divergence of cichlids in the great lakes of Africa, most species of which inhabit the relatively narrow band along the shoreline and have extremely restricted dispersal abilities. However, it does not account for the low diversity of cichlids in African rivers (54). In addition, radiation of other lacustrine taxa is not limited to diversification in shoreline habitats (55). Moreover, in the oceans, some types of speciation and evolutionary diversification occur more readily in open, two-dimensional habitats than along continental shelves (56).

8) Least action effect: Speciation occurring after the initial burst usually involves a minimum phenotypic change.

This pattern is explained by the joint action of genetic constraints and selection for local adaptation: As each lineage gets more specialized for a particular ecological niche, it becomes more and more difficult to establish adaptations for alternative niches (25, 26). The widely observed pattern of phylogenetic niche conservatism, in which closely related species are ecologically and phenotypically similar, is consistent with this pattern (57, 58).

9) Effect of the number of loci: Rapid and extensive diversification is most likely if the number of underlying loci is small.

This is one of the most general patterns emerging from a variety of models (20, 25, 26). A smaller number of loci implies that their individual contributions to the traits are larger, the effect of selection on each locus is stronger, the number of genetic changes necessary for divergence is smaller, and recombination and migration are less efficient in destroying the coadapted combinations of genes that emerge during speciation. This prediction is supported by data on cichlids, finches, and monkeyflowers, all of which indicate the existence of a small number of loci underlying traits involved in ecological interactions and reproduction (59–61).

10) Porous genome effect: Species can stably maintain their divergence in a large number of selected loci for very long periods despite substantial hybridization and gene flow that decreases or removes differentiation in neutral markers.

This effect has been observed in many different models (25, 26). A related prediction is that during earlier stages of diversification, when reproductive isolation is still weak, new traits (ecological or involved in mating) that emerge in some lineages can spread to other lineages as a result of hybridization.

Botanists have long been aware that sympatric and ecologically differentiated taxa can maintain their distinctiveness in the face of ongoing hybridization. Recent years, however, have shown that a similar pattern also occurs in many species of animals (62). Indeed, recent work has suggested that such interspecific gene flow can be an important source of genetic variation that enables adaptive diversification in early stages of radiation (11, 12).

On the other hand, the homogenizing effect of gene flow has classically been considered an impediment to evolutionary divergence (9), a role that it probably plays in many cases (63). Moreover, in some cases in which reproductive isolation is based on ecological differences among species, environmental perturbations can negate these isolating mechanisms, leading previously genetically distinct taxa to interbreed and even "de-speciate" (64).

General Conclusions

This brief survey suggests the following:

1) More empirical studies are needed specifically aimed at assessing the predictions discussed above. At present, we are left with a haphazard set of studies that happen to be relevant.

2) More generally, evolutionary biology is an inductive science in which we establish generalities by the accumulation of case studies. The number of adaptive radiations that have been extensively studied from the many different perspectives relevant to our discussions is surprisingly small. More detailed studies, integrating across a variety of approaches and disciplines, is needed to build a reservoir of case studies from which generalizations can be drawn.

3) We need studies of general models aiming to capture the most widespread patterns of adaptive radiation. At the same time, we need models that are more closely tailored to the biology of particular taxa. For example, some models (25, 26) assume that mating occurs in the ecological niche that a species exploits; this assumption is true for some taxa, such as some host-specific insect herbivores, but not for other classic adaptive radiations. The extent to which relaxing these assumptions or tailoring them to other biological situations (e.g., different species concepts) would change the predictions needs to be explored. The complexity of the processes of adaptive radiation is reflected in the complexity of corresponding mathematical models. Using the emerging tools of high-performance computing will be crucial for better understanding of models (and nature).

Darwin was confronted with the fruits of adaptive radiation throughout his 5-year journey around the world, and their evolutionary exuberance made an impression on him. Speaking of the Galápagos finches that now bear his name, he wrote in *The Voyage of the Beagle*:

"Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species has been taken and modified for different ends."

In the 150 years since publication of the *Origin*, adaptive radiations have continued to astonish and inspire scientists and the public alike. But how exactly radiation occurs, and how it differs among taxa and in different settings, as well as why some lineages radiate and others do not, are still unclear. Most likely this is because there is no single answer: Lineages vary in manifold ways, various evolutionary factors act simultaneously, similar evolutionary outcomes can be achieved via alternative paths, and the contingencies of place and time play a large role in guiding the evolutionary process.

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REVIEW

Evidence for Ecological Speciation and Its Alternative

Dolph Schluter

Natural selection commonly drives the origin of species, as Darwin initially claimed. Mechanisms of speciation by selection fall into two broad categories: ecological and mutation-order. Under ecological speciation, divergence is driven by divergent natural selection between environments, whereas under mutation-order speciation, divergence occurs when different mutations arise and are fixed in separate populations adapting to similar selection pressures. Tests of parallel evolution of reproductive isolation, trait-based assortative mating, and reproductive isolation by active selection have demonstrated that ecological speciation is a common means by which new species arise. Evidence for mutation-order speciation by natural selection is more limited and has been best documented by instances of reproductive isolation resulting from intragenomic conflict. However, we still have not identified all aspects of selection, and identifying the underlying genes for reproductive isolation remains challenging.

It took evolutionary biologists nearly 150 years, but at last we can agree with Darwin that the origin of species, "that mystery of mysteries" (*1*), really does occur by means of natural selection (*2*–*5*). Not all species appear to evolve by selection, but the evidence suggests that most of them do. The effort leading up to this conclusion involved many experimental and conceptual advances, including a revision of the notion of speciation itself, 80 years after publication of *On the Origin of the Species*, to a definition based on reproductive isolation instead of morphological differences (*6*, *7*).

The main question today is how does selection lead to speciation? What are the mechanisms of natural selection, what genes are affected, and how do changes at these genes yield the habitat, behavioral, mechanical, chemical, physiological, and other incompatibilities that are the reproductive barriers between new species? As a start, the many ways by which new species might arise by selection can be grouped into two broad catego-

ries: ecological speciation and mutation-order speciation. Ecological speciation refers to the evolution of reproductive isolation between populations or subsets of a single population by adaptation to different environments or ecological niches (*2*, *8*, *9*). Natural selection is divergent, acting in contrasting directions between environments, which drives the fixation of different alleles, each advantageous in one environment but not in the other. Following G. S. Mani and B. C. Clarke (*10*), I define mutation-order speciation as the evolution of reproductive isolation by the chance occurrence and fixation of different alleles between populations adapting to similar selection pressures. Reproductive isolation evolves because populations fix distinct mutations that would nevertheless be advantageous in both of their environments. The relative importance of these two categories of mechanism for the origin of species in nature is unknown.

In this review, I summarize progress in understanding the general features of speciation by selection. I do not differentiate speciation by sexual selection here because natural selection drives the divergence of mate preferences, by either ecological or mutation-order mechanisms, in most

theories of the process (*8*, *11*). I leave out discussion of sympatric and allopatric speciation but instead identify the likelihood of ecological and mutation-order speciation when there is gene flow. I ignore reinforcement, a special type of natural selection thought to favor stronger premating reproductive isolation once postzygotic isolation has evolved. I also ignore speciation by polyploidy, even though selection might be crucial in the early stages.

Speciation and Adaptation from Darwin to Dobzhansky

Appreciation of the connection between adaptation and speciation began with Darwin when a morphological concept of species largely prevailed. In *On the Origin of Species*, Darwin wrote that "I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other..." and "The amount of difference is one very important criterion in settling whether two forms should be ranked as species or varieties" (*1*). Under this view, speciation is defined as the accumulation of sufficiently many differences between populations to warrant their classification as separate taxonomic species. Darwin understood the importance of reproductive barriers between species (*1*), but the study of speciation after the publication of this work focused mainly on the evolution of species differences, particularly of morphological traits but also of behavioral and other phenotypic traits.

Under this Darwinian perspective, linking speciation with adaptation was relatively straightforward, requiring only a test of whether phenotypic differences between species were caused by natural selection. For example, at the American Association for the Advancement of Science 1939 speciation symposium [the last major symposium on speciation before the biological species concept (*7*)], an extensive comparative and biogeographic study showcased instances in which derived morphological and life history forms of fishes had arisen over and over again from the same ancestral type (*12*). The repeated, parallel origin of non-parasitic lamprey in streams from the same migratory, parasitic ancestor showed that "Again and

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