# I.19

# Adaptive Radiation
## Rosemary Gillespie

Adaptive radiation is generally triggered by the appearance of available niche space, which could result from (1) *intrinsic factors* or key innovations that allow an organism to exploit a novel resource, and/or (2) *extrinsic factors*, in which physical ecological space is created as a result of climatic changes or the appearance de novo of islands. There are no general rules as to what taxa are more likely to undergo adaptive radiation, although some lineages may have certain attributes that facilitate adaptive radiation in the appropriate setting. The process of adaptive radiation is described below, as well as some prime examples of the phenomenon. Adaptive radiation is generally initiated by expansion of ecological amplitude of a taxon into newly available ecological space, followed by specialization, the process possibly facilitated through adaptive plasticity. Speciation associated with adaptive radiation may involve one or more of the following: founder events, divergent natural selection, sexual selection, and hybridization. Competition is generally implicated in divergent natural selection and in dictating the communities of species formed during the course of adaptive radiation. Current research is focused on (1) examining the molecular underpinnings of apparently complex morphological and behavioral changes that occur during the course of adaptive radiation, and (2) experimental manipulation of bacteria to assess the conditions under which adaptive radiation occurs.

**GLOSSARY**

**adaptive radiation.** Rapid diversification of an ancestral species into several ecologically different species, associated with adaptive morphological, physiological, and/or behavioral divergence

**attenuation.** Decline in number of species represented on islands with distance from a source of colonists

**divergent natural selection.** Selection arising from environmental forces acting differentially on phenotypic traits (morphology, physiology, or behavior) resulting in divergent phenotypes; reproductive isolation may occur as a side effect, either in sympatry or allopatry

**ecological character displacement.** Divergence in ecological traits (which may lead to reproductive isolation as a by-product) caused by competition for shared resources

**ecological release.** Expansion of habitat or use of resources by populations into areas of lower species diversity with reduced interspecific competition

**ecological speciation.** Process by which barriers to gene flow evolve between populations as a result of ecologically based divergent natural selection

**ecomorph.** A group of populations, species, etc., whose appearance is determined by the environment

**escalation/diversification.** Diversification of a herbivore/parasite in concert with its host in which the adaptations of the host to counter exploitation by the herbivore or parasite build one on each other, and vice versa

**escape and radiation.** Diversification of a herbivore/parasite in concert with its host in which the host is generally considered to radiate before exploitation and subsequent radiation by the herbivore or parasite, and vice versa

**founder event.** Establishment of a new population with few individuals that contain a small, and hence unrepresentative, portion of the genetic diversity

relative to the original population, potentially leading to speciation

**key innovation.** Any newly acquired structure or property that permits the occupation of a new environment, or performance of a new function, which, in turn, opens a new adaptive zone

**nonadaptive radiation.** Elevated rate of speciation in the absence of noticeable ecological shifts

**sexual selection.** Form of natural selection based on an organism's ability to mate such that individuals with attributes that allow them greater access to the opposite sex, either through (1) combat with the same sex or (2) attributes that render them more attractive to the opposite sex, mate at higher rates than those that lack these attributes

**taxon cycle.** Temporal sequence of geographic distribution of species from (1) colonizing to (2) differentiating to (3) fragmenting and to (4) specializing

Adaptive radiation is the rapid diversification of a lineage into multiple ecologically different species, generally associated with morphological or physiological divergence. The phenomenon can be characterized by four criteria: common ancestry, a phenotype–environment correlation, trait utility, and rapid speciation. The concept of adaptive radiation, and particularly diversification of ecological roles by means of natural selection, has had a long history, beginning with the observations of Charles Darwin on the Galápagos Islands, and has played a pivotal role in the development of the Modern Synthesis (see Givnish and Sytsma, 1997, for a detailed history of the concept).

## 1. CONDITIONS PROMOTING ADAPTIVE RADIATION

The most familiar present-day adaptive radiations are known from isolated archipelagoes or similar island-like settings (e.g., lakes). However, it is quite likely that much of the diversity of life originated through episodes of adaptive radiation during periods when ecological space became available for diversification. Within this context there are two primary mechanisms through which ecological space can become available: (1) intrinsic changes in the organism often associated with key innovations, and (2) extrinsic effects, including environmental change and colonization of isolated landmasses. The two situations may be linked; for example, an intrinsic change may allow an organism to exploit a new environment. In either case, individuals exploiting the newly available niche space must be isolated to some extent from the remainder of the population to allow for genetic divergence associated with adaptive radiation. If a new habitat becomes available in close proximity to other such habitats (not isolated),

it will be colonized repeatedly by taxa from those habitats, and patterns of species diversity will be governed by ecological processes of immigration and extinction, rather than by evolutionary processes.

## Intrinsic Factors: Key Innovations

A key innovation is a trait, or a suite of traits, that allows an organism to exploit a novel resource or increase the efficiency with which a resource is used, thereby allowing a species to enter a "new" adaptive zone; the ecological opportunity thus provided may permit diversification. For example, the evolution of C4 photosynthesis, which enhanced rates of carbohydrate synthesis in open environments, likely served as a key innovation preceding radiation of most of the major lineages of grasses. Among recent adaptive radiations, one of the best-known key innovations is that of the pharyngeal jaw apparatus of cichlid fish (figure 1). Although most bony fishes have pharyngeal gill arches modified to process prey, the cichlid pharyngeal jaw is unique in having upper pharyngeal jaw joints, a "muscular sling," and suturing that functionally fuses the lower pharyngeal jaw. The features of the jaw appear to have allowed cichlids to exploit a diversity of prey types, including large fish and hard-shelled prey that are unavailable to most other aquatic vertebrates. In flowering plants, floral spurs have evolved at least seven times, each time resulting in higher rates of diversification, perhaps the best known radiation being in the columbines (*Aquilegia*, Ranunculaceae).

Interacting species, such as herbivores or parasites and their hosts, may themselves create ecological opportunity and provide some notable examples of key innovations. Here, the host may develop a defense to the herbivore or parasite (e.g., a plant may develop toxicity), but in due course the herbivore or parasite may develop resistance to the defense of the host. Paul Ehrlich and Peter Raven (1964) examined such coevolutionary responses and hypothesized that when plant lineages are temporarily freed from herbivore pressure via the origin of novel defenses, they enter a new adaptive zone in which they can undergo evolutionary radiation. However, if a mutation then arises in a group of insects that allows them to overcome these defenses and feed on the plants, the insect would then be free to diversify on the plants in the absence of competition. The major radiations of herbivorous insects and plants may have arisen through repeated steplike opening of novel adaptive zones that each has presented to the other over evolutionary time. Often referred to as escape and radiation, the host is generally considered to radiate before exploitation and subsequent radiation by the herbivore or parasite. This idea has been supported by
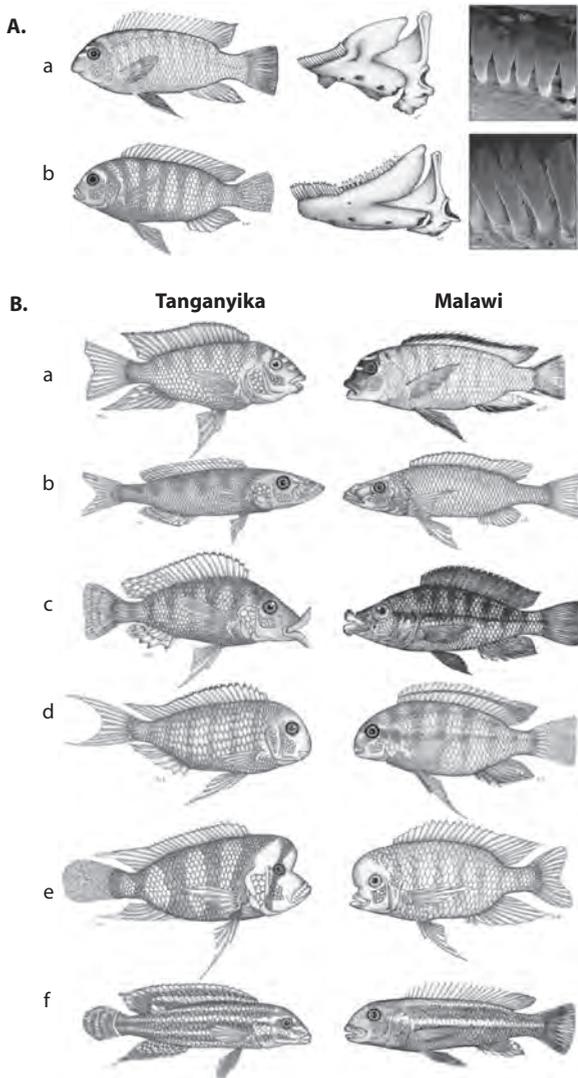
**Figure 1.** Adaptive radiation in cichlid fish. The pharyngeal jaw morphology, which allows dietary specialization, appears to have served as a key innovation in facilitating adaptive radiation in this group. (A) Biting and sucking species exhibit distinct morphologies. *Labeotropheus fuelleborni* (top) is a specialized biting species characterized by a short, robust lower jaw and an outer row of closely spaced tricuspid teeth. *Metriaclima zebra* (bottom) forages with a sucking mode of feeding and has a more elongate jaw and an outer series of larger bicuspid teeth. (B) Cichlids exhibit remarkable evolutionary convergence. Similar ecomorphs have evolved repeatedly within different cichlid assemblages. All of the cichlids in the left-hand column are from Lake Tanganyika. All of the cichlids in the right-hand column are from Lake Malawi and are more closely related to one another than to any species within Lake Tanganyika. Note the similarities among color patterns and trophic morphologies. (From Albertson, R. C., and T. D. Kocher. 2006. Genetic and developmental basis of cichlid trophic diversity. Heredity 97: 211–221, http://www.nature.com/hdy/journal/v97/n3/full/6800864a.html)

more recent studies of insect diversification in the context of their host plants, with repeated evolution of angiosperm feeding in phytophagous beetles associated with an increased rate of diversification. There is a consistently greater diversity of beetles among plants in which latex or resin canals have evolved as protection against insect attack. In the same way, adaptive radiation of parasites may occur as a consequence of host switching to a new lineage of hosts.

The development of a symbiotic association can also serve as a key innovation, providing a possible avenue through which taxonomic partners can enter into a new set of habitats unavailable to one or both of the symbiotic partners alone. For example, the development of gut endosymbionts and the concomitant ability to digest cellulose in ruminants appear to have led to the radiation of bovids in the African savannas. Likewise, the presence of algal endosymbionts has played a major role in the evolution and diversification of certain clades of Foraminifera.

## Extrinsic Factors

Rates of speciation are frequently accelerated with the physical appearance of new habitat (figure 2). In particular, changes in the temperature or humidity of the environment over various eras have repeatedly resulted in mass extinctions coupled with the opening of ecological space (see also figure 4). For example, the Cretaceous–Paleocene boundary event resulted in numerous extinctions of plants and insects and set the stage for the subsequent adaptive radiation of other groups. Environmental changes appear to form the basis of the Phanerozoic revolutions. Rising temperature and nutrient supplies as a result of submarine volcanism may have triggered later Mesozoic and perhaps early Paleozoic diversification episodes. Similar factors may underlie the iterative radiations of ammonoids through the geological record in which each radiation appears to have originated from a few taxa, which then went on to give rise to a wealth of morphological diversity.

The emergence de novo of isolated habitats can be considered a kind of environmental change, as, for example, the formation of islands in the ocean, and many adaptive radiations are associated with such situations. For example, the adaptive radiation of finches in the Galápagos Islands appears to have been triggered by the appearance of land through volcanic activity over the last 3 million years. As the number of islands increased, so did the number of finch species. In the same way, adaptive radiations in the Hawaiian Islands are mostly associated with the volcanic activity that resulted in the formation of the current high islands that date back approximately 5 million years. Likewise, the
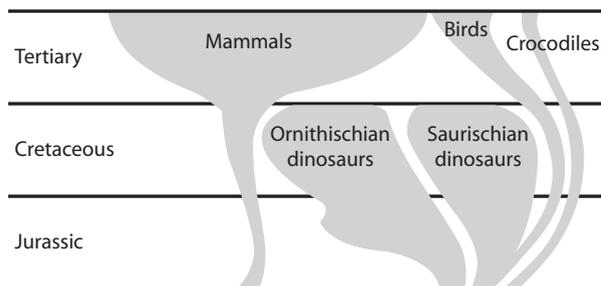
**Figure 2.** Open niches vacated by dinosaur extinctions at the end of the Cretaceous may have created empty ecological space and allowed mammals to radiate into these positions. Likewise, lineages that colonize isolated islands may give rise to adaptive radiations because the colonists are free from competition with other species. (From Understanding Evolution, http://evolution.berkeley.edu/evolibrary/article/side_o_0/adaptiveradiation_01)

evolution and adaptive radiation of the African cichlids appears to have been initiated in Lake Tanganyika approximately 5–6 million years ago when rivers in the area became progressively more swampy, with diversification of fish being initiated when river species became isolated in the deepening lake. In each of these cases, the new habitats were extremely isolated, resulting in infrequent colonization, thus giving the few successful colonists sufficient time to "explore" the ecological space available and diversify into multiple species.

## 2. ARE CERTAIN TAXA MORE LIKELY TO UNDERGO ADAPTIVE RADIATION?

Whether some species are predisposed to undergo adaptive radiation because of a broad environmental tolerance, generalized feeding patterns, or perhaps some proclivity to develop novel associations has been the subject of much debate. For example, birds have undergone extensive adaptive radiation in the insular Pacific, whereas butterflies have not. This has led some authors to suggest that speciation in butterflies may be constrained by the mechanics of insect–plant coevolution preventing rapid diversification in the insects. However, this argument is not well supported, as other insects with similar coevolutionary ties have undergone some of the most spectacular insular adaptive radiations known. It appears that, given conditions of isolation and time, almost any group of organisms is capable of undergoing adaptive radiation given ecological opportunity that it can exploit. However, certain groups do appear to be predisposed to adaptive radiation. For example, the occurrence of parallel radiations of sister clades of plants, the Hawaiian silverswords and California tarweeds, suggests that this lineage has certain

attributes that facilitate adaptive radiation in the appropriate settings.

## 3. EXAMPLES OF CURRENT ADAPTIVE RADIATIONS

Adaptive radiation has now been documented in every kingdom of life and in a large number of phyla and in many different circumstances. However, the original concepts were developed through studies on islands, as these systems are discrete and amenable for studying the basis of adaptive radiation. The earliest groups to be examined in this context were vertebrates, in particular birds, with perhaps the best-known example being that of the Galápagos finches (figure 3) initially described by John Gould, and used by Charles Darwin as a key demonstration of his theory of evolution by natural selection. Currently, there are 13 recognized species in three lineages: ground finches, tree finches, and warbler-like finches, with sympatric species occupying distinct ecological roles. Research by Peter and Rosemary Grant and colleagues has shown that the finches have considerable genetic variation within populations, which is intermittently subject to both natural and sexual selection, with the final community of finches on an island dictated by food resources and interspecific competition for these resources. In the Hawaiian Islands, the endemic honeycreepers, which show even more extraordinary morphological and ecological differentiation than the Galápagos finches, comprise 56 species in a single lineage. However, only 22 species of honeycreeper are currently extant, with others known only from historical or fossil collections, making it difficult to develop hypotheses regarding processes underlying the adaptive radiation. Other well-known vertebrate radiations include lizards (anoles) in the Greater Antilles of the Caribbean in which diversification has allowed species to occupy a range of ecological roles, with as many as 11 species occurring sympatrically. Different species live, for example, on twigs, in the grass, or on tree trunks near the ground. Jonathan Losos and colleagues recognize six types of habitat specialists on the basis of morphological measurements (see plate 4). Among frogs, a remarkable example of adaptive radiation has recently been found in Madagascar. Among mammals, the best-known adaptive radiation is also from Madagascar, where lemurs constitute a spectacular diversification of more than 65 species, although at least 15 of these are now extinct. In addition, some striking radiations of small mammals have been documented, including the rodents on the islands of the Philippines and bats in southeast Asia.

Additional spectacular examples of adaptive radiation in vertebrates come from lacustrine fish, with the best known being cichlids (mentioned above), which
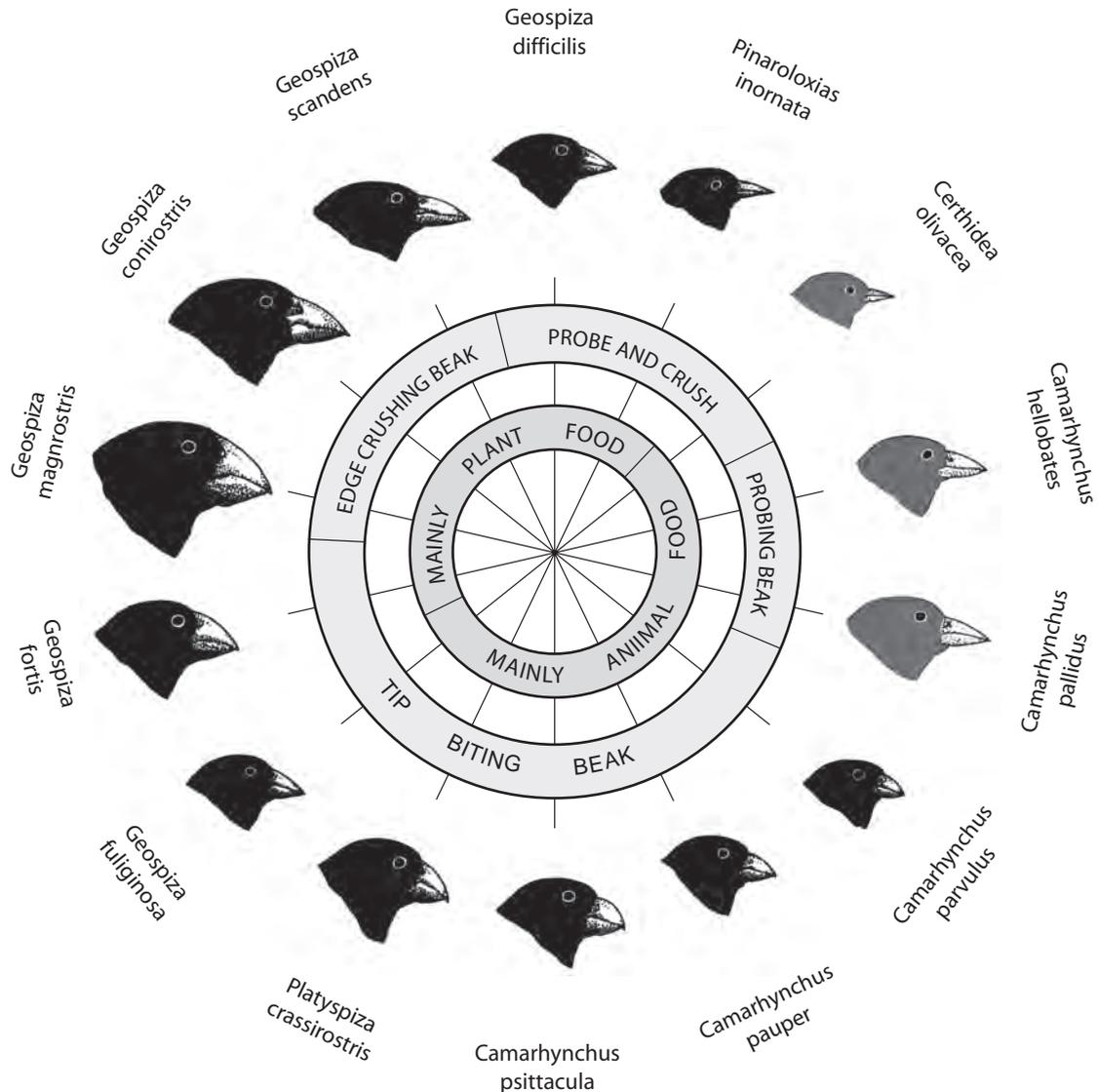
**Figure 3.** Adaptive radiation in Darwin's finches. Diagram illustrating the morphological and associated ecological diversity among the radiation of Darwin's finches in the genus *Geospiza* (Emberezidae). The 14 species evolved from a common ancestor about 3 million years ago. (From Grant, P. R., and B. R. Grant. 2008. How and Why Species Multiply: The Radiation of Darwin's Finches. Princeton, NJ: Princeton University Press)

reach their highest diversity in the East African lakes of Victoria (over 400 species), Malawi (300–500 species), and Tanganyika (approximately 200 species). In each of these lakes, the fish exhibit diversity in trophic morphology, including specialist algal scrapers, planktivores, insectivores, piscivores, paedophages, snail crushers, and fin biters. In addition to their trophic diversity, they display a striking array of color patterns, which appear to be involved in courtship and recognition. Other fish radiations include darters of the Central Highlands of eastern North America and threespine sticklebacks in deglaciated lakes in Canada. The latter in particular have now been heralded as an outstanding example of recent and ongoing adaptive radiation, within which it is possible to study processes involved. No more than two species occur in any one lake, but pairs of species in different lakes appear to have evolved independently of other pairs as a result of parallel bouts of selection for alternate trophic environments.

Among invertebrates, there are now a number of examples that show adaptive radiation associated with historic climatic change (figure 4). One of the best known ongoing radiations in insects is that of the Hawaiian *Drosophila* flies, in which courtship behavior can be very elaborate; the males of the so-called picture winged species often have ornately patterned wings as well as unusual modifications of the mouthparts and legs. At the same time, clades are characterized according to whether they breed on fungi, leaves, fruit, or bark, suggesting a role of both sexual selection and ecological shifts in allowing diversification of these flies. Hawaiian swordtail crickets have become increasingly recognized over recent years as a striking example of a very rapid island radiation. In common with other crickets, courting males "sing" to attract females by rubbing their forewings together. Each species has a unique song, and females respond preferentially to the song of the same species. Differentiation appears to occur through sexual selection on genetically well-structured populations. Among spiders, several radiations have been described in the Hawaiian Islands, one of the largest being in the genus *Tetragnatha*, where ecomorphs have arisen independently in much the same way as Caribbean lizards. In other parts of the Pacific, the land snail genus *Partula* is particularly well known for its radiation on different islands in the South Pacific. Like other land snails, they are highly polymorphic with respect to the color, banding, and chirality of the shell; competition appears to be important in dictating the array of species at a site. The Canary Islands are also well known for adaptive radiations of insects (in particular, beetles and psyllids) and spiders. Here, although most groups show evidence of competition in shaping communities, there is little biogeographic congruence between groups; stochasticity in species arrival patterns plays a prominent role in dictating species composition on any one island.

The Hawaiian silversword alliance (Asteraceae) has been considered a prime example of adaptive radiation in plants (plate 3). It consists of 28 species, which exhibit a large diversity of life forms, including trees, shrubs, mat-plants, monocarpic and polycarpic rosette plants, cushion plants, and vines, that occur across a broad environmental spectrum, from rainforests to desert-like settings. Additional plant radiations include columbines (mentioned above) in North America and numerous other island radiations, such as *Argyranthemum* in the Canary Islands and *Psiadia* in the Mascarenes, both of which are in the same family as the Hawaiian silverswords (Asteraceae) and have diversified in a parallel fashion.

One of the most recently described adaptive radiations is that of the soil bacterium *Pseudomonas fluor-escens*, which, over a short period of time, can develop from an isogenic population under conditions of environmental heterogeneity into several somewhat predictable ecomorphs. Accordingly, this system has been hailed as one within which it is possible to conduct experimental studies of adaptive radiation.

## 4. INITIATION OF ADAPTIVE RADIATION

Although there have been many studies that describe different adaptive radiations, the initiation of the process remains poorly understood. Yet it is possible to recognize some general patterns.

### Dispersal and Colonization

Because adaptive radiation requires colonization and differentiation in an ecologically available space, the taxa that colonize must necessarily be few. Although there appears to be a substantial random element to colonization, successful colonization of very isolated locations generally requires high dispersal abilities. Accordingly, representation of taxa within biotas in isolated areas will be skewed toward those that can disperse readily. For example, as one ventures farther into the Pacific Ocean from west to east (i.e., toward greater isolation), there is an attenuation in the number of lineages of terrestrial groups that have colonized by over-water dispersal. In less isolated archipelagoes, such as Fiji, the fauna is relatively rich with numerous continental affinities. Farther east, Samoa is less rich at higher taxonomic levels than Fiji but still has many families and orders that are lacking from the native fauna of more remote Polynesian islands. East of Samoa, the number of floral and faunal groups that have been able to reach the remote islands diminishes, and here the few colonists have frequently undergone adaptive radiation, accentuating the unrepresentative nature of the biota. The Hawaiian archipelago (4000 km from the nearest continent, North America; 3200 km from nearest island group) demonstrates this pattern most acutely: among insects, the native fauna is represented by only 50% of insect orders and 15% of known families and exhibits extraordinarily high levels of endemism (95–99% in invertebrates) with numerous cases of adaptive radiation.

High dispersal of colonists clearly contrasts with the apparently much restricted ranges and dispersal abilities that are frequently associated with members within an adaptive radiation. In general, there appears to be a dramatic loss of dispersal ability and/or attainment of a more specialized habitat at the outset of adaptive radiation. Indeed, a tendency toward reduced dispersal following colonization of new ecological space
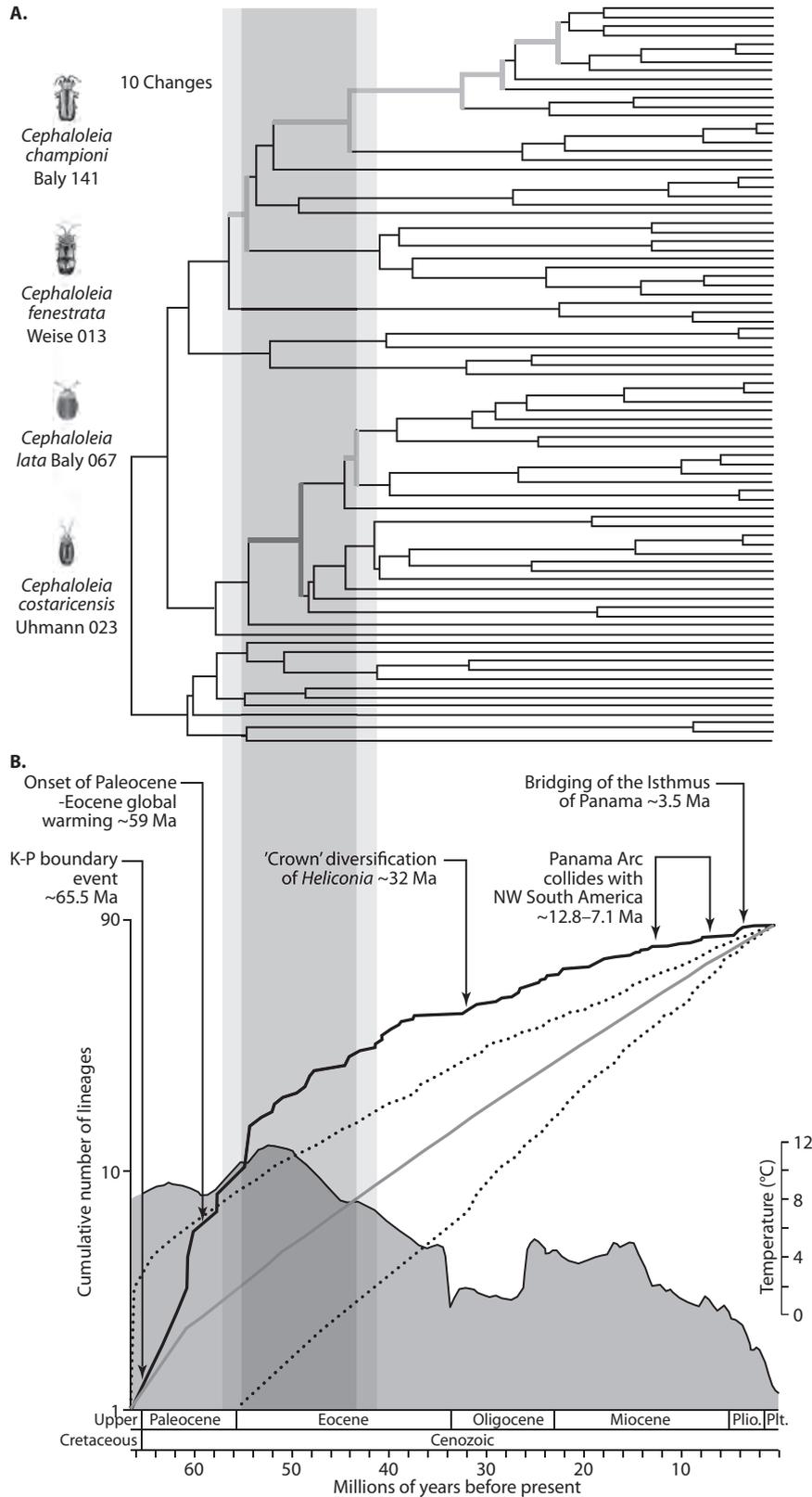
**A.**

10 Changes

*Cephaloleia championi* Baly 141

*Cephaloleia fenestrata* Weise 013

*Cephaloleia lata* Baly 067

*Cephaloleia costaricensis* Uhmann 023

**B.**

Onset of Paleocene -Eocene global warming ~59 Ma

K-P boundary event ~65.5 Ma

'Crown' diversification of *Heliconia* ~32 Ma

Bridging of the Isthmus of Panama ~3.5 Ma

Panama Arc collides with NW South America ~12.8–7.1 Ma

Cumulative number of lineages

90

10

1

Temperature (°C)

12

8

4

0

Upper Cretaceous | Paleocene | Eocene | Oligocene | Miocene | Plio. | Plt.

Cenozoic

60        50        40        30        20        10

Millions of years before present

**Figure 4.** Tempo in the adaptive radiation of *Cephaloleia* (Coleoptera: Chrysomelidae). (A) Chronogram showing significant diversification rate shifts (each terminal corresponds to a species) and source(s) of support. Shading indicates the timeframe over which significant diversification rate shifts occurred. (B) Semilogarithmic plot of lineages through time (LTT) for *Cephaloleia* (LTT plot; heavy upper line) superimposed on a time-averaged record of high-latitude sea-surface temperatures (lower irregularly descending line), a proxy for global climate. The constant diversification rate model is rejected if the empirical LTT curve falls outside the 95% confidence interval generated by simulation (middle ascending lines). Upturns or downturns in the empirical LTT plot reflect changes in rates of speciation or extinction. (From McKenna, Duane D., and Brian D. Farrell. 2006. Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. Proceedings of the National Academy of Sciences U.S.A. 103: 10947–10951)

may be an important factor in allowing diversification to proceed.

### Ecological Release and Specialization

When a taxon first colonizes a new area, it frequently expands its ecological range, a phenomenon referred to as ecological release. Regular cycles of ecological and distributional change following colonization of islands are well known—the phenomenon was described first in detail for Melanesian ants and subsequently for Caribbean birds. The idea is that widespread, dispersive populations or species (Stage I) give rise to differentiating (Stage II) and then fragmented (Stage III) and ultimately specialized endemic species (Stage IV). This pattern is consistent with the early stages of adaptive radiation. However, once local endemics have formed, there appears to be little evidence to suggest that species become progressively more specialized over time. Phylogenetic analysis of some radiations suggests that specialized species, when they colonize new habitat, may be able to expand their range and accordingly may reinitiate the "cycle" to give rise to other specialist species.

### Behavioral Plasticity

Although it has been suggested that behavioral and ecological plasticity may impede adaptive diversification as it allows a single taxon to exploit a broad environmental range, recent research suggests otherwise. Mary Jane West-Eberhard (2003) has argued that adaptive plasticity (including behavior) promotes evolutionary diversification, in particular when the environment is variable. Recent theoretical work has supported this idea, and plasticity has now been suggested as playing a role in a number of radiations. For example, in Caribbean anoles, plasticity may allow species to occupy a new habitat in which they otherwise might not be able to survive. Once in these habitats, their behavior may become modified, and, as new mutations arise, selection may act to accentuate the initial, relatively minor, morphological changes.

Conclusive demonstration that phenotypic plasticity precedes, and then permits, subsequent evolution has been difficult to obtain because once the ancestral populations have evolved, they may lose the pattern of plasticity present at the start of adaptive differentiation. In the threespine stickleback, however, where ancestral oceanic sticklebacks likely have changed little since colonization and diversification of freshwater species, the pattern of behavioral plasticity in the ancestral species supports the argument that phenotypic plasticity can guide subsequent evolutionary change and facilitate adaptive radiation.

## 5. SPECIATION IN ADAPTIVE RADIATION

Rapid speciation coupled with phenotypic diversification are key features of adaptive radiation, and accordingly, many studies have examined the basis for genetic diversification. Because adaptive radiation involves ecological shifts, divergent natural selection has been most broadly implicated across a spectrum of lineages, with founder effects and sexual selection also playing a role in certain situations. However, the mechanism through which species form during adaptive radiation is still only very poorly understood, although it appears that geographic barriers to gene flow are generally involved at least in the initiation of speciation.

### Founder Events

A founder event refers to the establishment of a new population by a few individuals that carry only a small sample of the genetic diversity of the parent population. Many studies have suggested that founder events can play a role in adaptive radiation, as taxa within a radiation often have very small population sizes, with ample opportunity for isolation. Because of the effects of random sampling, a founder event will lead to differences in allele frequencies at some loci as compared to the parent population. However, considerable debate has focused on the nature of genetic changes that occur subsequent to the founder event, during the period of population growth, with some traditional arguments suggesting that founder events trigger rapid species formation, although more recent studies have largely refuted a role for founder events in reproductive isolation. Genetic drift can lead to changes during the bottleneck, but the effect becomes weaker as the population starts to grow. At the same time, a large proportion of alleles are lost during a bottleneck, and few new mutations can occur while the population size is small. The effect of these opposing forces is that the number of beneficial mutations fixed per generation remains largely unchanged by the bottleneck. Nevertheless, selection subsequent to a genetic bottleneck can preserve alleles that are initially rare and that would otherwise tend to be lost as a result of stochastic events in populations of constant size.

### Divergent Natural Selection

As with other factors considered to play a key role in adaptive radiation, competition plays a dual role. On the one hand, reduced competition is generally associated with the presence of open resource niches, either as organisms move into new habitats or through the acquisition of a key innovation, thereby providing in-

creased opportunities for diversification. On the other hand, competition, often with ecological character displacement, is frequently implicated in promoting adaptive change between close relatives. However, there are no known direct tests that link the evolution of reproductive isolation to interspecific competition, and the role of competition in the early stages of adaptive radiation remains unclear. Nevertheless, divergent natural selection driven by interspecific competition appears to have shaped current phenotypic differences in many radiations ranging from sticklebacks in the Canadian lakes to lizards on the islands of the Caribbean, finches in the Galápagos, and spiders in the Hawaiian Islands.

Predation has also been suggested as a possible operative that may work together with (or instead of) competition to allow adaptive differentiation, but this has been difficult to test. However, the specific role of predation in facilitating adaptive radiation has recently been demonstrated in both walking-stick insects and bacteria.

Sexual selection (see below) has been shown in some cases to act in concert with divergent natural selection. For example, sexual dimorphism in Caribbean anole lizards allows a species to exploit different niches, thereby serving as an alternative means of ecological diversification.

### Hybridization and Gene Flow

Gene flow among populations in the process of diverging, or hybridization between incipient species, may slow the process of diversification and homogenize populations. However, interspecific hybridization may also be a possible source of additional genetic variation within species: Hybridization increases the size of the gene pool on which selection may act and therefore may be a significant process in the adaptive radiation of some species. Such effects have now been shown in Darwin's finches, African cichlids, Lake Baikal sculpins, and several lineages of Hawaiian plants.

### Sexual Selection

Sexual selection has been implicated in the diversification of species within some of the most explosive adaptive radiations. In particular, it has been suggested that sexual selection drives species proliferation in Hawaiian *Drosophila* flies and *Laupala* crickets. The mechanism for this, as proposed by Kenneth Kaneshiro and colleagues for *Drosophila,* is that, when a newly founded population is small, female discrimination is relaxed; accordingly, sexual behavior becomes simpler with more intraspecific variability. Divergence of sibling species may then occur during isolation as a result

of a shift in the distribution of mating preferences. In Hawaiian *Laupala* crickets, closely related species are morphologically similar with no ecologically recognizable features and distinguishable only by the pulse rate of the male courtship song, a secondary sexual trait used in mate attraction. These crickets demonstrate the highest rate of speciation recorded so far in arthropods.

Other taxa in which extreme diversification has been attributed in part to sexual selection include haplochromine cichlids, in which sexually dimorphic breeding coloration, with brightly colored males and often dull females, appears to have arisen through female mate choice for male coloration. Disruptive sexual selection on male coloration can result in genetic isolation between fish that exhibit small differences in male coloration and female preference for male coloration. Likewise, diversification in jumping spiders in the sky islands of the western United States appears to be the product of female preference for greater signal complexity or novelty.

In all of these radiations, ecological differentiation still occurs, but sexual selection may act somewhat independently and accelerate the rate of differentiation. Mate choice is the primary isolating mechanism, and hybrids between rapidly diverging sibling species are often fully viable and fertile.

## 6. COMMUNITY ASSEMBLY

During the course of adaptive radiation, speciation plays a role similar to that of immigration, although over an extended time period, in adding species to a community. It appears that when a lineage diversifies in a community, it may adapt to multiple different ecological settings, with the development of specific sets of attributes, or ecomorphs, to match a given microhabitat. In an archipelago situation, where similar habitats occur on different islands, it has been found that similar sets of ecomorphs can arise independently within the same lineage through convergent evolution, a phenomenon first demonstrated in anole lizards in the Caribbean (plate 4) and now shown in a wide range of other adaptive radiations including Himalayan birds, Galápagos finches, cichlid fish of the African rift lakes, Canadian lake sticklebacks, ranid frogs in Madagascar, spiders in the Hawaiian islands, and snails in the Bonin Islands of Japan. These results point to a model of ecological community assembly that incorporates evolutionary effects of interspecific competition.

The central importance of competition in shaping communities has recently been challenged by Stephen Hubbell's "neutral theory," which postulates that differences between members of a community of ecologically equivalent species are "neutral" with respect to

their success. One outcome of neutral theory has been to prompt investigation of when, and to what extent, ecological equivalence might play a role. In the course of adaptive radiation, neutral processes may govern the identity of taxa initially colonizing a new area, potentially resulting in a transient period with multiple ecological equivalents. Likewise, communities formed through sexual selection may include some ecologically similar species. However, the end product of subsequent ecological speciation appears inevitably to be a set of taxa that are ecologically distinct.

## 7. MOLECULAR BASIS FOR ADAPTIVE CHANGE

That repeated evolution of similar forms has occurred in many species undergoing adaptive radiation has led to considerable research on the molecular underpinnings of such apparently complex changes. With the development of molecular techniques, we now have the opportunity to analyze the genetic architecture of species differences and the role of new mutations versus standing genetic variation in adaptation and divergence in adaptive radiation. For example, in fish, it appears that gene duplication provided a genomic mechanism for adaptive radiation of teleosts, with lineages arising after duplication being much more species-rich than the more basal groups. Studies on the body plating in a radiation of sticklebacks have shown that related alleles are responsible for a given phenotype, indicating that even though a given phenotype (ecomorph) may have multiple independent origins, the same ancestral allele appears to be involved in producing the same phenotypes.

In groups in which sexual selection has been implicated in diversification, investigation of rapidly evolving genes for traits associated with sex and reproduction have been the target of research on the process of speciation. For *Drosophila*, results show differential patterns of evolution of genes expressed in reproductive and nonreproductive tissues, supporting the role of sexual selection as a driving force of genetic change between species.

## 8. TESTING ADAPTIVE RADIATION

Experimental tests of the processes underlying adaptive radiation are now possible using microbial systems to probe the relative roles of niche space, competition, predation, and time in dictating when and how adaptive radiation occurs. These studies, although still in their infancy, have shown many parallels between adaptive diversification of bacterial genotypes over the space of a few weeks and the presumed early stages of adaptive radiation of macroorganisms over millions of years. The challenge is to apply the knowledge gained from these rich bacterial systems to a more general understanding of adaptive radiation.

## FURTHER READING

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