Chapter 15

Adaptive Radiation: The Interaction of Ecological Opportunity, Adaptation, and Speciation

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Darwin may have been the first to describe adaptive radiation when, contemplating the variety of finches that now bear his name, he remarked: "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" (Darwin 1845: 380). Since Darwin's time, naturalists and evolutionary biologists have been fascinated by the extraordinary diversity of ecology, morphology, behavior, and species richness of some clades, but interest in adaptive radiation has surged in recent years, largely as a result of three developments.

First, evolutionary ecologists have focused on the mechanisms that produce adaptive radiation. Careful study of ecological divergence within and among populations has yielded a wealth of information about how natural selection leads to evolutionary diversification (Schluter 2003; Nosil and Crespi 2006; Grant and Grant 2008a) (Figure 15.1). Schluter's (2000) seminal work, *The Ecology of Adaptive Radiation* was a watershed in the field, building upon and extending in important ways Simpson's (1953) *The Major Features of Evolution* published a half-century earlier.

Second, the explosion of molecular phylogenetics in the last two decades (see Hillis, Chapter 16) has revealed the diversification histories of countless clades and has provided the raw material for a renaissance of adaptive radiation studies. Molecular research has offered surprising discoveries about the history and magnitude of many adaptive radiations, such as the vangids of Madagascar (Yamagishi et al. 2001) (Figure 15.2), the corvoids of Australia (Sibley and Ahlquist 1990; Barker et al. 2004), the cichlids of Lake Victoria (Meyer et al. 1990; Seehausen 2006), the lobeliads of Hawaii (Givnish et al. 2009) and a plethora of others. In each of these cases, the great ecological and morphological diversity of a group had been thought to be the result of independent colonization events from multiple, differently adapted ancestral lineages. Instead, new molecular phylogenies revealed

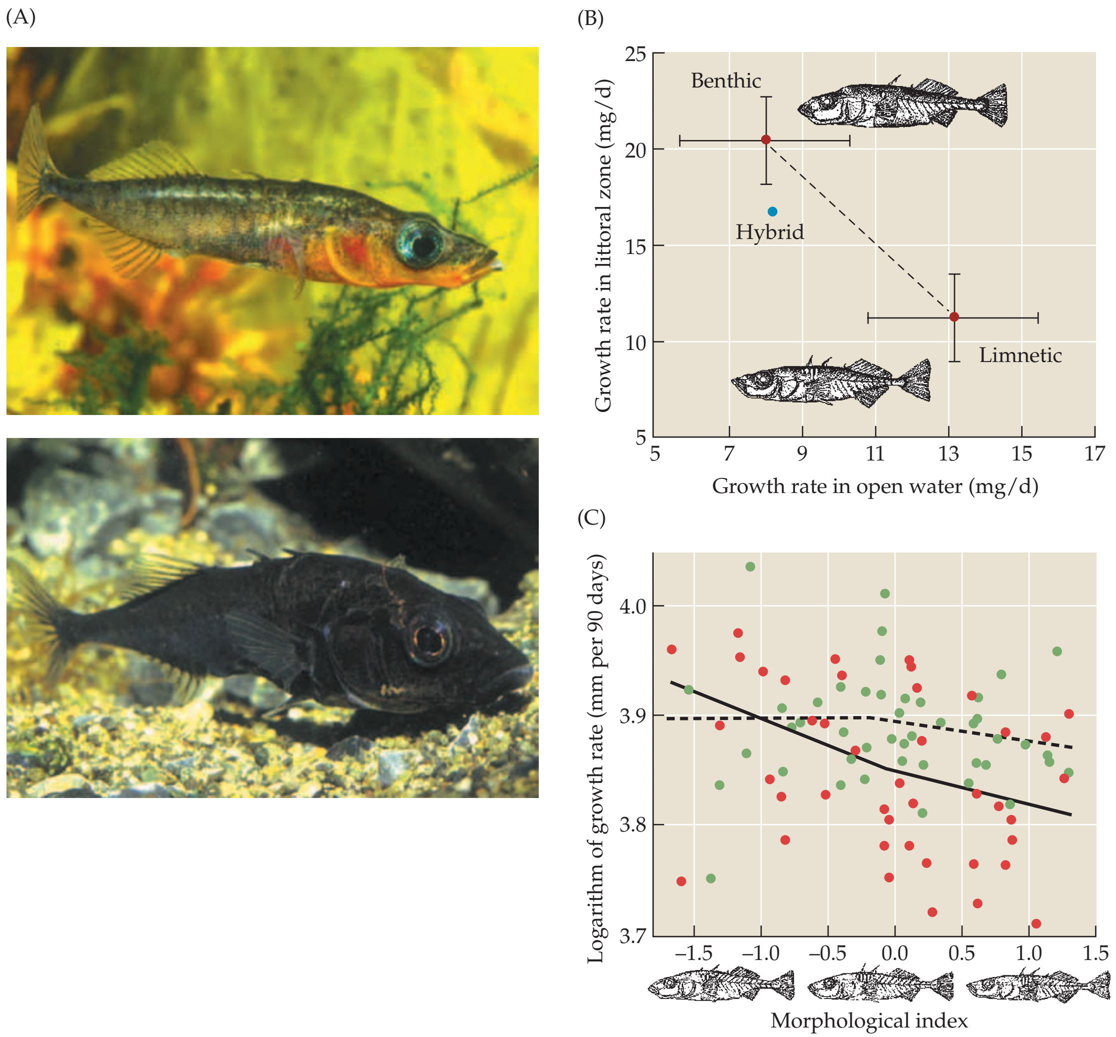


FIGURE 15.1 Natural Selection and Adaptation in British Columbian Threespine Sticklebacks (*Gasterosteus aculeatus*) (A) A number of lakes in British Columbia contain two species of sticklebacks, one that is slender-bodied, with a small mouth, eats zooplankton, and occupies open water (limnetic, above); the other is larger, deeper-bodied, has a large mouth, and eats invertebrates near the lake bottom (benthic, below). (B) Each species has higher growth rates in its own habitat, and hybrids are inferior in both habitats. (C) Natural selection (using growth rate as a proxy) on a highly variable hybrid population favors more benthic-like individuals in the presence of the limnetic species (red dots and solid line), but not in their absence (green dots and dashed line). Such studies have shed light on the role of ecology and natural selection in driving divergence during adaptive radiation. (A, from Rundle and Schluter 2004, photos © Ernie Cooper; B, adapted from Schluter 1995; C, adapted from Schluter 1994.)

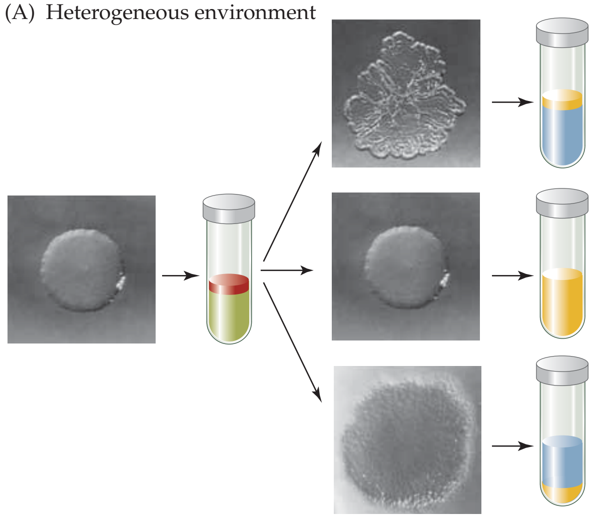
FIGURE 15.2 Malagasy Vangids Molecular phylogenetic study indicates that the vangids represent a monophyletic group, rather than being members of several different families with closest relatives elsewhere. (From Yamagishi et al. 2001.)

that the great diversity in these groups is the result of *in situ* evolution, that is, adaptive radiation (see references previously cited).

Not only have many previously unknown adaptive radiations been discovered with molecular data, but also time-calibrated phylogenetic trees of extant taxa allow classic hypotheses of adaptive radiation to be tested in new ways (Glor 2010). Previously, the primary way to estimate the tempo of macroevolution was to measure it directly using high-quality paleontological data (see Wagner, Chapter 17), which are available for relatively few lineages. However, nucleotide sequence data now provide an alternative means of reconstructing phylogenetic relationships and the timing of lineage divergence events. With time-calibrated phylogenies, one may ask questions such as whether the occurrence of adaptive radiation is correlated with historical events (e.g., mass extinctions, changes in climate) or whether the pace of diversification decreases through time, as often is expected of an adaptive radiation (Box 15.1).

Third, experimental studies of microbial evolution have added a new dimension to the study of adaptive radiation (see Dykhuizen, Commentary 2). Such studies bring the benefits of experimental control, large sample sizes and replication, and the ability to not only track lineages through the diversification process, but also to freeze ancestral taxa and subsequently resurrect them to interact with their descendants (Lenski and Travisano 1994). Although thus far primarily based on studies of short-lived asexually reproducing organisms diversifying under simplified ecological conditions (a situation that is changing), microbial evolution studies have permitted experimental tests of many of the basic hypotheses of adaptive radiation, allowing microevolutionary processes to be directly and experimentally connected to macroevolutionary outcomes and often confirming predictions of the adaptive radiation model (Kassen 2009) (Figure 15.3).

(A) Heterogeneous environment



(B) Homogeneous environment

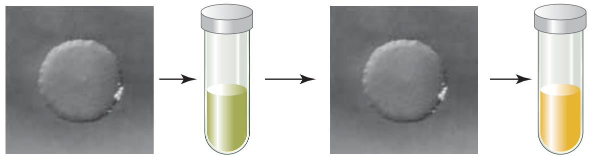


FIGURE 15.3 Experiments on the Evolutionary Diversification of the Bacterium *Pseudomonas fluorescens* Resources were distributed either heterogeneously (solution with red and green strata in A) or homogeneously (uniform green solution in B) distributed. After several days, bacteria in the heterogeneous environments repeatedly diverged into the same three morphotypes, which interact negatively and differ in resource use (the yellow shading on the right depicts typical resource use for each morphotype; the different forms tend to thrive as a surface film, in solution, or along the substrate, respectively). By contrast, only one morphotype occurred in the homogenous treatment. (Adapted from Rainey and Travisano 1998.)

BOX 15.1
TESTING FOR CHARACTERISTIC PATTERNS OF ADAPTIVE RADIATION

With time-calibrated phylogenies, researchers can investigate whether lineage diversification patterns match patterns expected from the ecological process of adaptive radiation. These approaches focus on how the pace of lineage or phenotypic diversification alters over time or with changing ecological conditions, such as ecological opportunity. The most common approach to testing for the signature of adaptive radiation is to construct models in which parameters describe changes in the tempo of diversification as a result of ecological conditions. Alternative ecological models may be compared to each other, to non-ecological models, or to a null model in which diversification proceeds at a constant rate.

Tests for the signature of adaptive radiation have a rich pedigree in quantitative paleontology, in which numerous studies have tracked the rise and fall of diversity and disparity in relation to mass extinction events, the evolution of key innovations, and colonization of new regions (Simpson 1953; Sepkoski 1978; Foote 1997, 1999; reviewed in Erwin 2007; see Foote, Chapter 18) (Figure 1A,B).

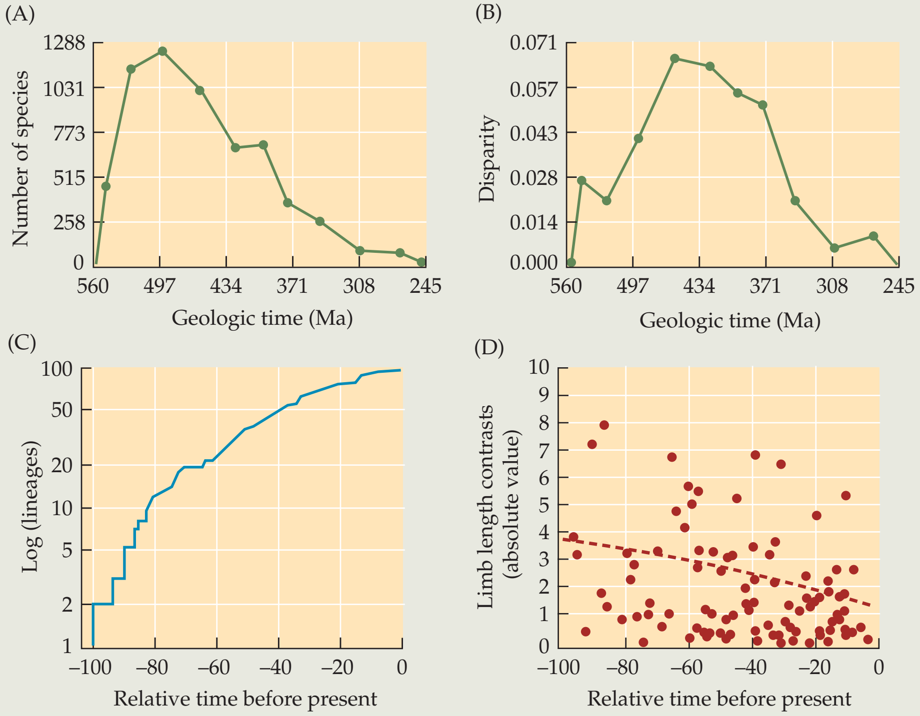


FIGURE 1 The "Early Burst" Pattern of Adaptive Radiation In the fossil record, an early burst may be detected by tracking the number of species and the total disparity of a radiation over geological time. In trilobites, species richness (A) and disparity (B) both peaked early in the history of the clade. Phylogenetic comparative methods may be used to detect an early burst from data on extant taxa. Greater Antillean *Anolis* lizards exhibit both a rapid early accumulation of lineages, depicted as a concave lineages-through-time plot in (C), as well as an early burst in phenotypic evolution, evident as larger independent contrasts early in the radiation (D). (A,B adapted from Foote 1993; C,D adapted from Mahler et al. 2010.)

(continued)

BOX 15.1 *Continued*

The most commonly used phylogenetic test evaluates the early burst model, in which early diversification is explosive as lineages rapidly adapt to new ecological roles but slows as opportunities disappear due to ecological saturation (Nee et al. 1992; Rabosky and Lovette 2008; Phillimore and Price 2009; reviewed in Glor 2010). The majority of tests of the "early burst" model have investigated patterns of lineage diversification, but similar models have recently been developed for phenotypic traits as well (Freckleton and Harvey 2006; Agrawal et al. 2009; Harmon et al. 2010, in press; Mahler et al. 2010, in revision) (Figure 1C,D). Support for this model varies—the common finding of temporally declining lineage diversification has led some to proclaim a strong role for ecological opportunity in regulating cladogenesis, although the sample of clades studied may be biased (McPeek 2008; Phillimore and Price 2008; Ricklefs 2009). Among phenotypic studies of the early burst model (which, to date, are far fewer than studies focusing on species richness), some studies report declining rates of evolution with diminishing ecological opportunity (Freckleton and Harvey 2006; Agrawal et al. 2009; Mahler et al. 2010, in revision), whereas Harmon et al. (2010) find only limited support for the early burst model in a wide survey of animal radiations.

A key feature of the model-fitting approach is the flexibility provided by the variety of models that may be compared when evaluating adaptive radiation hypotheses. In addition to the early burst model, a diversity of alternative models are available for fitting data, including radiation under flexible ecological limits, radiation with high lineage turnover, and radiation in stages, among others (Price 1997; Harvey and Rambaut 2000; McPeek 2008; Benton 2009; Gavrilets and Vose 2009; Rabosky 2009). The ability to identify patterns of adaptive radiation using phylogenetic methods is likely to improve in coming years as new and more refined models are developed.

In this chapter, we review what is known about the mechanisms that drive adaptive radiation and, more importantly, highlight those areas requiring further research. Along the way, we will discuss what constitutes an adaptive radiation and how one can be identified.

Evolutionary Radiation: What Are the Types, How Are They Recognized, and Are They Special?

Adaptive radiations draw the attention of scientists and non-scientists alike because their grandeur seems to imply that something special is responsible: these groups are extraordinary and require explanation, invocation of some special attribute, either intrinsic or external, that can explain why these particular clades have diversified to such an extreme extent (Box 15.2). But, adaptive radiation describes only one part of the spectrum of evolutionary radiations. Although distinguishing among types of evolutionary radiation may involve making arbitrary distinctions (Olson and Arroyo-Santos 2009), doing so provides a useful framework for further study of the key features of radiations.

BOX 15.2
ARE ADAPTIVE RADIATIONS EXCEPTIONAL?

We suggest that the term adaptive radiation should be reserved for those clades exhibiting exceptional ecological and phenotypic disparity (see Figure 15.4). The rationale for this argument is that it is the unusually great degree of disparity in these clades that requires explanation—by identifying such clades, researchers can focus on them to understand what has triggered their extraordinary evolutionary diversification. Implicit in this approach is the need to develop statistical methods to separate those clades that constitute adaptive radiations from those that do not.

This approach can be criticized on two counts. First, it creates an arbitrary dichotomy in what is most likely a continuous distribution (Olson and Arroyo-Santos 2009). That is, the degree of adaptive disparity of clades is surely continuously distributed. How can one draw a line and say that all clades with a greater amount of disparity than the threshold constitute adaptive radiations and that all with even a slightly lesser amount, are not?

An alternative approach to the threshold-based approach would be to quantify disparity for a sample of clades and investigate whether the degree of disparity is statistically related to a factor, such as degree of ecological opportunity (presuming it could be quantified), that has been hypothesized to drive adaptive radiation. Increasingly, tools for investigating the relationship between such factors and patterns of ecological diversification are being developed and employed (Olson and Arroyo-Santos 2009; Glor 2010).

The second criticism of this definition of adaptive radiation is based on the view that adaptive radiation is a process as well as an outcome (just as one might argue that adaptation is both a process and an end-result). This argument suggests that the same processes are involved in adaptive diversification whether the result is an enormous adaptive radiation, such as African Rift Lake cichlids, or a small clade of species slightly morphologically differentiated to adapt to minor differences in habitat use. Because both cases are the result of the same process of cladogenesis plus adaptive divergence driven by natural selection, this view would suggest that all such clades, no matter how disparate, should be considered adaptive radiations.

Such a view would render the term adaptive radiation meaningless. The vast majority of clades are composed of species that exhibit at least a small degree of phenotypic disparity that has arisen as a result of adaptive divergence driven by natural selection. Assuming this is true, almost all clades would be adaptive radiations, and the term would have little utility in identifying clades of special interest. We feel that this not only neuters the term "adaptive radiation," but also departs from its use throughout the history of evolutionary biology.

One way out of this problem might be to restrict the term adaptive radiation to clades in which adaptive diversity arose in a burst of evolution early in a clade's history, with subsequent deceleration in the rate of evolution. Indeed, many definitions of adaptive radiation include the proviso that radiation must occur quickly (Givnish 1997). This view, however, also has problems. Either the definition must include clades that achieve only modest disparity as long as they accumulated it early, or it must rely on an arbitrary disparity threshold.

From our perspective and that of many others (Givnish 1997), the important aspect of adaptive radiation is the disparity produced by the clade (Foote 1997; Erwin 2007), rather than the pace at which it accumulates. In some models of adaptive radiation (Harvey and Rambaut 2000), an adaptive radiation may unfold at a rather steady pace; indeed, ecological opportunity may ap-

(continued)

BOX 15.2 *Continued*

pear suddenly in some cases (e.g., colonization of an unoccupied island) but more gradually in others (e.g., co-radiation with another clade). We prefer to reserve the question of timing of diversification as a hypothesis to be tested among adaptive radiations, rather than a criterion for deciding whether a clade constitutes an adaptive radiation or not. At the least, if one takes the more restrictive definition that includes timing, then another term is needed for those clades that produce exceptional disparity but in a non-explosive way, perhaps such as Simpson's (1953) mostly forgotten "progressive occupation of adaptive zones."

Evolutionary radiation results in the production of two components of diversity—species richness and phenotypic diversity (often termed "disparity" to avoid confusion with "species diversity"). Adaptive radiation is a type of evolutionary radiation, emphasizing the extent of phenotypic differentiation among members of a clade as species adapt to use different ecological resources; we henceforth refer to this as "adaptive disparity." Although a wide variety of definitions of adaptive radiation have been proposed (Givnish 1997), Futuyma's (1998) definition seems to capture the sense of most of these: "evolutionary divergence of members of a single phylogenetic lineage into a variety of different adaptive forms." More specifically, we propose that the term adaptive radiation should refer to those clades that exhibit an exceptional extent of adaptive disparity. Definitional issues and methods for identifying adaptive radiations are reviewed in Box 15.3.[1]

Much of the literature on evolutionary radiations equates species richness with adaptive radiation. Indeed, many of the world's most remarkable and celebrated radiations are rich in both species and adaptive form, including the African Rift Lake cichlids, Hawaiian *Drosophila*, Caribbean *Anolis* lizards and, at a higher level, beetles and angiosperms. Such lineages undoubtedly represent adaptive radiations and suggest that species proliferation and ecological radiation occur hand in hand. Although often true, this need not be the case.

Some clades are exceptionally diverse phenotypically and constitute adaptive radiations, despite having unexceptional species diversity (Figure 15.4). For example, the lizard clades Pygopodidae and Cordylidae both contain great ecological and morphological disparity despite being species poor (Webb and Shine 1994; Branch 1998). Groups such as these are commonly neglected in studies of adaptive radiation, but deserve more attention, particularly in studies of the role of speciation in adaptive radiation (see subsequent discussion).

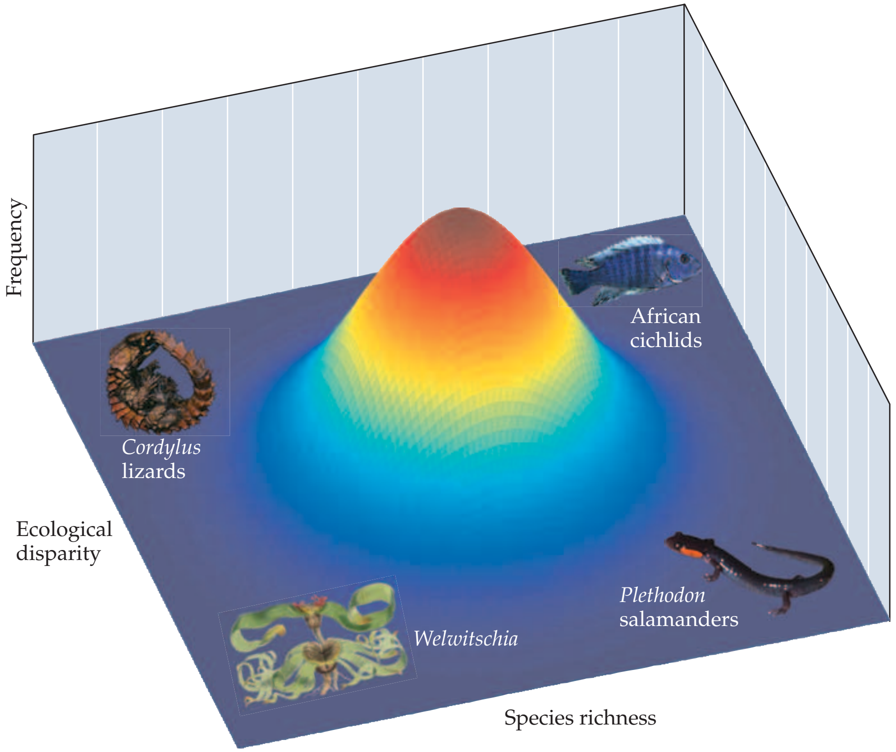


FIGURE 15.4 The Axes of Evolutionary Radiation Clades can be diverse in both species richness and ecological variety, termed disparity. Clades that have exceptional ecological disparity are adaptive radiations, whether they have great (e.g., African lake cichlids) or little species richness (e.g., cordylid lizards). Non-adaptive radiations are those that are exceptional in species richness, but not in ecological disparity, such as plethodontid salamanders. Some clades are exceptionally non-disparate and species-poor, such as *Welwitschia*.

Conversely, other clades contain a great number of species, but little ecological or phenotypic disparity. For example, the eastern North American slimy salamanders (*Plethodon*) are a species-rich clade that diversified rapidly early in their evolutionary history. However, these salamander species are distributed almost entirely allopatrically and are ecologically similar (Kozak et al. 2006). Such clades have been termed non-adaptive radiations (Gittenberger 1991; Kozak et al. 2006; Rundell and Price 2009). Great species richness without substantial phenotypic disparity could arise if a clade was predisposed to speciate in ways that do not involve adaptive divergence, as might result from allopatric isolation in similar environments or from the operation of sexual selection occurring in divergent ways in different populations.

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[1] Integral to the concept of adaptive radiation is the concept of adaptation itself. Evolutionary divergence can occur for reasons other than adaptive differentiation. Thus, investigation of the adaptive basis of trait differentiation is essential in any study of adaptive radiation. Arnold (1994), Larson and Losos (1996), and McPeek, Commentary 3 (in this volume) provide reviews of adaptation and how it can be studied. For the purposes of discussion here, we will assume that phenotypic differences among species are adaptively based.

BOX 15.3
METHODS FOR IDENTIFYING EXCEPTIONAL CLADES

If exceptional diversity is a key feature of adaptive radiation, statistical methods are needed that can test whether a radiation is exceptional. Such a test must demonstrate that a clade contains more disparity than would be expected under a neutral model of diversification, or that it is exceptionally disparate compared to other radiations.

In principle, such questions could be addressed either by examining the fossil record or by using phylogenetic methods. Both of these methods have advantages and disadvantages. Paleontological methods directly track changes in diversity over time. By contrast, with phylogenetic methods using extant taxa, macroevolutionary changes must be inferred. As such, results arising from these methodologies are only as sound as their assumptions, and inadequate models for reconstructing evolutionary history may lead to both Type I and Type II errors in testing adaptive radiation hypotheses (Revell et al. 2005; see Foote, Chapter 18). Paleontological studies incorporate extinct taxa, and although phylogenetic methods exist for estimating the influence of extinction (Nee et al. 1994; Kubo and Iwasa 1995), they often suffer from low statistical power (Bokma 2009; Quental and Marshall 2009; Rabosky 2009). In contrast, the phylogenetic approach has several distinct advantages. In particular, phylogenetic studies permit investigation of long-term evolutionary patterns in taxa that are also well-studied ecologically—inferences about the ecology of fossil taxa can be unreliable, particularly when the taxa do not have comparable extant counterparts, and morphological homoplasy may also undermine accurate estimation of the relationships of fossil taxa in paleontological studies. Moreover, the quality of the fossil record varies greatly among taxa; phylogenetic methods can be used even for taxa with little or no fossil record. Of course, the most reliable insights into the large-scale pattern of adaptive radiation will be those that are well supported by both paleontological and phylogenetic investigations.

Statistical approaches to the identification of exceptional clades have concentrated almost entirely on patterns of lineage diversification rather than phenotypic diversification. The first lineage diversification models, in which speciation occurred as a uniform stochastic process, produced surprising results (Raup et al. 1973; Slowinski and Guyer 1989). The resulting phylogenies tended to be topologically unbalanced, suggesting that large differences in clade species richness could occur by chance alone (Guyer and Slowinski 1993; Barraclough and Nee 2001; Nee 2001, 2006). Nonetheless, many clades in the Tree of Life are exceptionally species-rich (or species-poor), even compared to the highly variable neutral expectation. For instance, at a very broad scale, Alfaro et al. (2009) identified nine such clades among all vertebrates.

Of course, while such lineage diversification models are useful for testing whether species radiations are exceptional, they do not necessarily identify adaptive radiations, which are distinguished by ecological and morphological disparity. Paleontologists have long used measures of disparity to trace patterns of phenotypic evolution through time, and changes in disparity in fossil lineages have been pivotal in testing and refining adaptive radiation theory in recent decades (Foote 1997; Roy and Foote 1997; Ciampaglio et al. 2001; Erwin 2001, 2007).

To date, few studies of extant taxa have attempted to identify those clades that are exceptionally disparate using phylogenetic methods (Losos and Miles 2002). Direct comparisons of disparity among taxa are problematic, because disparity is a function of the rate of evolution, the age of a clade, and the phylogenetic topology of the clade (O'Meara et al. 2006) (Figure 1). One approach is to estimate the rate of phenotypic evolution in a phylogenetic context and to compare rates among clades (Collar et al. 2005; Harmon et al. 2008; Pinto et al. 2008).

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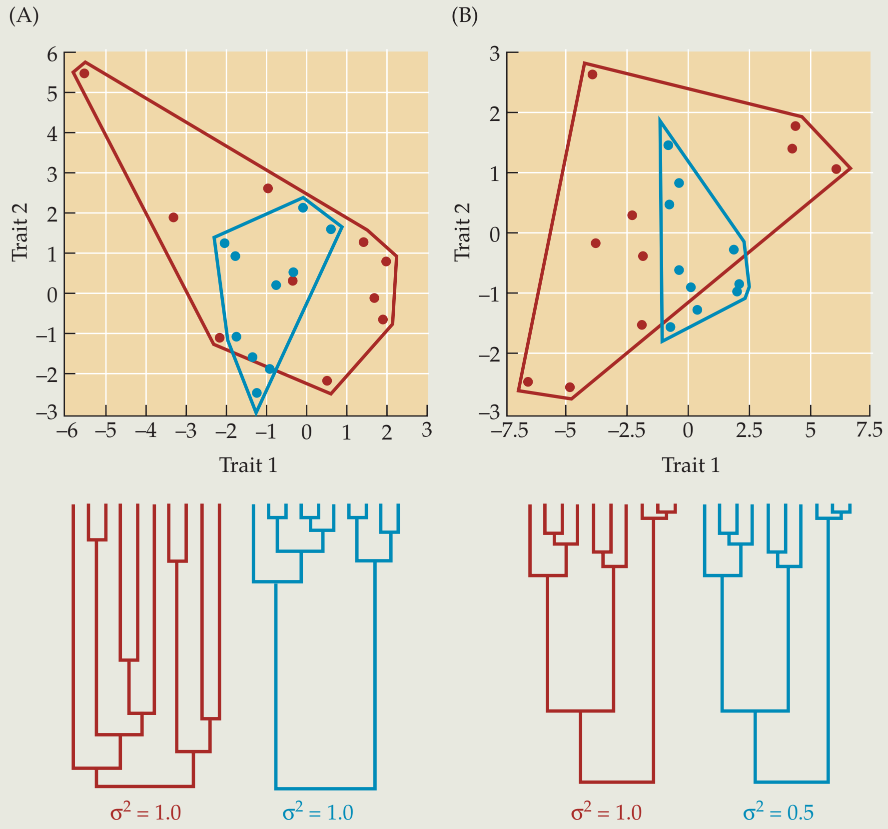

FIGURE 1 The Effect of Phylogenetic Structure and Rate of Evolution on Expected Disparity Under a Brownian motion model of evolution, disparity among extant taxa is a function of the rate of phenotypic evolution as well as of the structure of the phylogenetic tree relating those taxa. In (A), a phenotypic trait evolved at a constant rate on phylogenetic trees that were identical in branching order, but different in the relative timing of divergence. In the first phylogeny, lineage diversification was concentrated early, while in the second phylogeny, lineage divergences were concentrated late. Although the rate of trait evolution was the same for each phylogeny, greater disparity resulted when divergences were concentrated earlier, because traits evolved independently for longer periods of time. In (B), a trait evolved on identical phylogenies, but the rate of evolution (σ^2) differed by a factor of two between the two phylogenies. In this case, when the rate of evolution was higher, trait disparity was greater. In both (A) and (B), disparity differences are depicted graphically, using minimum convex polygons for the evolved trait values, and data in the upper panels are colored to match the phylogenies and rates under which they were generated.

Ecological Opportunity and Adaptive Radiation

The idea that ecological opportunity is a necessary prerequisite for adaptive radiation dates to Simpson (1953) who argued that an ancestral species must find itself in a setting in which "the [adaptive] zone must be occupied by organisms for some reason competitively inferior to the entering group or must be empty" (Simpson 1953: 207). More recently, Schluter (2000) suggested that ecological opportunity is "loosely defined as a wealth of evolutionarily accessible resources little used by competing taxa" (Schluter 2000: 69).

An ancestral species might find itself in the presence of ecological opportunity for a number of reasons:

1. colonization of isolated areas with a depauperate biota, such as islands, lakes, or mountaintops;
2. arrival or evolution of a new type of resource;
3. occurrence in a post-mass extinction environment, again with a depauperate biota;
4. evolution of a feature that provides the species with access to available resources that were previously unattainable; such a feature is referred to as a key innovation[2].

Many of the most famous examples of adaptive radiation occur on islands, including such iconic radiations as Darwin's finches, Hawaiian honeycreepers and silverswords, and *Anolis* lizards. Lakes, the terrestrial counterparts of islands, host additional renowned radiations, such as the African Rift Lake cichlids and the many radiations in Lake Baikal. One notable feature of many island radiations is that in the absence of many types of organisms normally found in mainland settings, members of the radiation have adapted in a wide variety of different ways, using resources that on the mainland are utilized by taxa not present on the island (Carlquist 1974; Leigh et al. 2007; Losos and Ricklefs 2009). The absence of many types of predators on islands may also play a role, by allowing organisms to use resources and habitats previously unavailable because of predation threat (Carlquist 1974; Schluter 1988; Benkman 1991). As a result, the ecological and phenotypic disparity of island radiations is often much greater than their mainland relatives (Carlquist 1974; Schluter 2000; Lovette et al. 2002; Figure 15.5). This oft-repeated phenomenon clearly indicates the role of ecological opportunity in spurring adaptive radiation.

Species may also experience ecological opportunity without moving to a new area if new resources appear, by immigration or evolution, where a

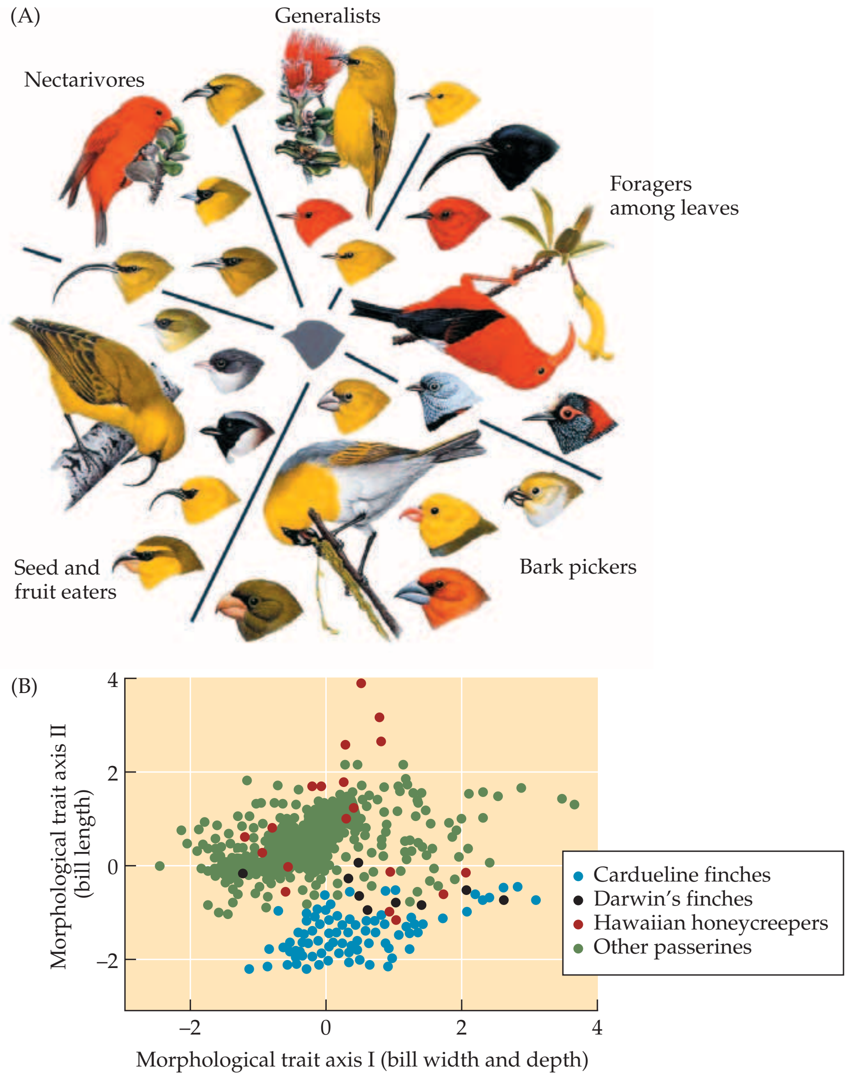

FIGURE 15.5 Adaptive Radiation of Island Birds (A) Hawaiian honeycreepers exhibit stunning morphological disparity in bill traits which corresponds to diversity in resource use. (B) The disparity of honeycreepers surpasses that of their mainland relatives, the cardueline finches and rivals that of all passerine birds. Another island radiation, Darwin's finches, also exhibits substantial disparity. In both island radiations, species occupy a diverse range of ecological niches utilized by species in many different families on the mainland. (A, reproduced with permission from Pratt 2005; B, adapted from Lovette et al. 2002 and Losos and Ricklefs 2009.)

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[2] A key innovation is defined as a trait that allows a species to interact with the environment in a fundamentally different way (Miller 1949; Liem 1974). For a critical discussion of the concept of key innovations, see Cracraft (1990) and Donoghue (2005). In recent years, the term has also been used to refer to a trait that increases the rate of species diversification (Heard and Hauser 1995; Hodges and Arnold 1995; Sanderson and Donoghue 1996; Ree 2005). This definition, however, introduces a different concept; conflating the two under the same name is confusing (Hunter 1998). A new term is needed for the latter phenomenon.

clade already occurs. For example, the radiation of horses is often attributed to the spread of grasslands in the Miocene (MacFadden 1992). Similarly, the plant genus *Espeletia* has radiated extensively in paramo habitats at high elevations in the northern Andes (Monasterio and Sarmiento 1991; Rauscher 2002; Hooghiemstra et al. 2006). The Andes are young, and presumably, the ancestral *Espeletia* rode the rising mountain chain, adapting to new high-elevation habitats as they appeared. Hughes and Eastwood (2006) infer a similar history for Andean *Lupinus*.

Ecological opportunity also appears in the aftermath of mass extinctions (Erwin 2001, 2007). Surviving taxa often radiate rapidly and relatively quickly attain similar disparity to that seen before the extinction event. In some cases, clades radiate into parts of morphological space that previously were unoccupied by members of that clade (Foote 1999), whereas in other cases a surviving subclade expands its disparity to encompass parts of morphological space previously occupied by other subclades that perished in the mass extinction (Foote 1996; see Foote, Chapter 18; Ciampaglio 2002; McGowan 2004; Friedman 2010). The high rates of phenotypic evolution exhibited after mass extinctions by these clades strongly support the role of ecological opportunity in spurring radiation.

The evolution of a key innovation can allow access to previously unattainable resources, providing the stimulus for adaptive radiation. For example, the evolution of wings in bats allowed them to prey upon a wide range of flying insects probably unavailable to their earthbound ancestors. Many other examples of key innovations have been proposed, although such hypotheses are usually difficult to test because they represent unique historical events. One way around this difficulty is to look for putative key innovations that have evolved multiple times to see if they have repeatedly led to adaptive radiation (Mitter et al. 1988; de Queiroz 2002); several examples, such as toe pads in lizards (Russell 1979; Larson and Losos 1996), phytophagy in insects (Mitter et al. 1988; Farrell 1998), wings in vertebrates, and pharyngeal jaws in fish (Stiassny and Jensen 1987; Mabuchi et al. 2007), seem to pass this test.[3] However, key innovations do not necessarily lead to adaptive radiation; the evolution of such a trait may allow the species to interact with the environment in new ways without leading to substantial evolutionary diversification (Fürsich and Jablonski 1984; Levinton 1988; de Queiroz 2002).[4] For example, aardvarks have evolved a suite of skeletal modifications permitting a termitophagous existence, but this specialization has not led to evolutionary diversification (Hunter 1998; see also Baum and Larson 1991 on *Aneides* salamanders).

Although not usually discussed in these terms, the evolution of mutualistic interactions may also function in a manner analogous to that of a key innovation by providing access to resources that were previously inaccessible (see Lane, Commentary 4). For example, the great diversity of herbivorous insects and vertebrates would not be possible if it were not for their mutualistic microbial gut inhabitants that allow them to digest cellulose (Janson et al. 2008). Similarly, the great variety among modern corals is likely in part the result of a mutualism between scleractinian corals and their endosymbiotic zooxanthellae, which provides photosynthetic energy in return for protection and nutrition (Stanley 1981).

The concept of ecological opportunity is straightforward and intuitive. Given the number of examples in which ecological opportunity (achieved in the four ways just enumerated) has led to adaptive radiation, there can be little doubt that it is an important trigger to adaptive radiation. Nonetheless, we may wonder whether ecological opportunity is a prerequisite for adaptive radiation.

Can Adaptive Radiation Occur in the Absence of Pre-Existing Ecological Opportunity?

Adaptive radiation could occur in the absence of pre-existing ecological opportunity either by members of a clade wresting resources away from other taxa that had been using them or by creating their own opportunity.

COMPETITIVE REPLACEMENT OF ONE CLADE BY ANOTHER Much of the older paleontological literature is peppered with proposals that one group has radiated by outcompeting another, usurping its resources and forcing it into evolutionary decline (e.g., the decline of mammal-like reptiles putatively as a result of the purported superiority of dinosaurs in locomotion or thermoregulation; Bakker 1968). However, very few of these cases hold up to close scrutiny. Usually, when one group replaces another ecologically similar group, the explanation is that the first group went extinct, followed by radiation of the second group (Rosenzweig and McCord 1991; Benton 1996; Brusatte et al. 2008). In a few cases, the fossil record does support the argument that one group has radiated at the expense of a clade that previously utilized the same resources. Perhaps, the best example is the interaction between cheilostome and cyclostome bryozoans, in which cheilostomes have outcompeted cyclostomes in local interactions over the course of many millions of years, all the while diversifying adaptively, while cyclostomes decreased in diversity (Sepkoski et al. 2000).

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[3] All of these examples are cases in which taxa with the putative key innovation exhibit substantially greater disparity than their sister taxa, although this observation has not been statistically tested. Instead, quantitative tests in these papers have compared species richness, rather than disparity.

[4] Similarly, it is possible that the evolution of the same key innovation could lead to radiation in some clades and not others, depending on the context in which it evolves. Consequently, failure to find a statistical relationship between evolution of a putative key innovation and adaptation radiation does not indicate the evolution of the trait did not lead to adaptive radiation in any of the clades in which it occurs (de Queiroz 2002).

This phenomenon of one group preventing evolutionary radiation of another has been termed niche incumbency and is seen in experimental microbial systems as well as in the fossil record (Brockhurst et al. 2007). It parallels the ecological phenomenon of the priority effect, which occurs when one species can prevent another from becoming established in a community by dint of prior occupancy (MacArthur 1972; Chase 2007). Moreover, the observation that the introduced invasive species almost never causes the global extinction of native species by outcompeting them[5] lends support to the idea that a radiating clade is unlikely to drive another clade to extinction through competitive interactions (Simberloff 1981; Davis 2003; Sax et al. 2007).

CAN ADAPTIVE RADIATIONS CREATE THEIR OWN OPPORTUNITY? It would seem, then, that ecological opportunity is usually necessary for adaptive radiation and that in most well-studied cases, such opportunity exists prior to adaptive radiation. However, a rarely considered alternative possibility is that lineages create their own opportunity as they radiate. Such self-propagation of an evolving radiation could occur in two ways.

First, as a clade radiates, the increased number of co-occurring clade members may create opportunities for exploitation by other species. The standard view among evolutionary biologists is that ecological opportunity decreases through the course of a radiation as niches are filled. However, an alternative view is that the more species that occur in a community, the more opportunity there is for other species to take advantage of them through predation, parasitism, mutualism, or other processes (Whittaker 1977; Tokeshi 1999; Erwin 2008). Most communities are composed of species from many different clades, but in cases (usually on islands) in which members of a single radiation are extremely diverse ecologically, the possibility exists for an evolutionary component to this view: as the clade radiates, it may create additional opportunities, spurring further radiation, thus creating further opportunities, and so on.

Implicit in this hypothesis is the view that interactions driving adaptive radiation occur not only as competition for resources, but also between species on different trophic levels. Indeed, adaptive radiations are known in which some members of the radiation prey on other members. Among African Rift Lake cichlids, for example, some species prey on others by eating their young, plucking their eyeballs, or rasping scales off their body. Social parasites in hymenopterans are often closely related and are sometimes the sister taxa of the species they parasitize, which is referred to as “Emery’s rule” (Bourke and Franks 1991; Savolainen and Vepsalainen 2003). These observations certainly indicate the possibility that adaptive radiations create additional opportunity as they unfold. Although Schluter (2000) suggested this idea a decade ago,[6] no empirical work has addressed this question; however, theoretical literature on the evolution of food webs is beginning to develop (Ingram et al. 2009).

Radiations may also be self-propagating when two clades co-radiate. Just as a clade may continually create its own ecological opportunity as it radiates, two clades may reciprocally generate opportunity for each other as they coevolve. Such coevolutionary radiations could take many forms. For example, the radiation of one group, perhaps driven by interspecific competition or predation, may create new ecological opportunities for a second clade that utilizes members of the first as a resource. In turn, radiation of the first group may continue if a species evolves some adaptation that frees it from attack by the second group, allowing it to utilize resources that were previously inaccessible. This last scenario is the basis of Ehrlich and Raven’s (1964) famous escape and radiation theory of plant–herbivore coevolution, and plays an important part in Vermeij’s (1987) theory of “evolution and escalation” between predators and prey. In other cases, co-radiations may simply result if species in one clade are each specialized to use a single member of a second clade; in this case, adaptive radiation in the host clade may be mirrored by radiation in their specialists. The recent divergence of the parasitic wasp, *Diachasma alloeum*, in response to divergence of its host, the apple maggot fly, *Rhagoletis pomonella*, illustrates how such matched divergence may unfold (Forbes et al. 2009). A similar process may have contributed to the extraordinary parallel radiations of figs and fig wasps as well as of *Glochidion* trees and *Epicephala* moths (Herre et al. 1996; Weiblen and Bush 2002; Kato et al. 2003).

As with the role of mutualism in adaptive radiation, the processes driving coevolutionary radiations are the same as in other radiations, but the synergistic interactions among co-radiating clades are distinctive. Such coevolutionary radiations may be particularly important in plant–herbivore systems (Farrell and Mitter 1994, 1998; Roderick and Percy 2008; Winkler and Mitter 2008; see Berenbaum and Schuler, Chapter 11).

Adaptive radiations may create their own opportunity in a second way: members of a radiating clade may alter their environment, creating ecological opportunities that did not previously exist. The concept of “ecosystem engineering” refers to the role that organisms play in altering their physical environment (Jones et al. 1994, 1997); ecosystem engineers, such as corals or rainforest trees, change the physical environment in ways that allow the existence of new species, potentially even leading to the evolution of ecological types that otherwise would not exist (Erwin 2008). Although several studies have documented that ecosystem engineering in one clade may trigger adaptive radiation in another clade (e.g., corals and tetraodontiform

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[5] The same is not true of introduced predators, which are responsible for scores of species extinctions (Davis 2003; Sax et al. 2007).

[6] And Wilson in 1992 proposed: “what I like to call the test of a complete adaptive radiation: the existence of a species specialized to feed on other members of its own group, other products of the same adaptive radiation” (Wilson 1992: 118).

fishes; Alfaro et al. 2007), few examples from nature document members of an adaptive radiation altering the environment in such a way to create ecological opportunities that have then been utilized by other members of their own radiation. One possible example is the evolution of lobeliad plants in Hawaii. Among the first plant clades to arrive and radiate in this archipelago, lobeliads diversified to fill ecological roles ranging from canopy trees to shrubs, epiphytes, and vines—one-eighth of the Hawaiian flora in total (Givnish et al. 2009). Given their early arrival and the extent of their ecological diversification, it is plausible that some lobeliads (e.g., shade-dependent shrubs) radiated in microhabitats created by other members of the radiation (e.g., woody trees), a hypothesis that could be tested with further phylogenetic analyses.

Laboratory studies of microbial adaptive radiation also support a role for ecosystem engineering driving diversification. Several studies have shown that the waste product of an ancestral microbial species created a food source subsequently used by a second type that evolved from its ancestor (Kassen et al. 2009).

Does "Ecological Opportunity" Have More than Heuristic Value?

The conclusion of the preceding discussion is that ecological opportunity is usually necessary for adaptive radiation, but whether we can predict *a priori* if a clade will radiate is not clear for two reasons. First, ecological opportunity, though usually necessary, may not be sufficient for radiation. Second, ecological opportunity may be extremely difficult to define objectively *a priori* and, as a result, the concept may have limited utility for predicting when clades would be expected to radiate adaptively, as opposed to explaining retrospectively why they did so.

Many clades fail to radiate despite apparently abundant ecological opportunity. For example, the Galápagos and Hawaii are famous for their bird radiations (finches and honeycreepers, respectively), but many other bird lineages on these islands have failed to produce adaptive radiations, including mockingbirds on the Galápagos (Arbogast et al. 2006) and thrushes on Hawaii (Lovette et al. 2002). The same is true of many other island taxa. Radiation may not occur in such circumstances for several reasons:

1. The perception of ecological opportunity may be mistaken.
2. Inability to access or utilize resources (e.g., from the lack of genetic variation or phenotypic plasticity that could produce phenotypes capable of taking advantage of novel available resources).
3. Lack of speciation: if, for some reason, speciation cannot occur (as discussed subsequently), then adaptive radiation cannot result.
4. Inability to diversify ecologically: even when speciation can occur, if the resulting descendant species are unable to diverge phenotypically to specialize on different resources, then a clade may not be able to radiate adaptively. Lack of such evolvability (Liem 1974; Vermeij 1974; Cheverud 1996; Wagner and Altenberg 1996; Gerhart and Kirschner 1998; Rutherford and Lindquist 1998; see G. Wagner, Chapter 8) may occur for a variety of reasons, often referred to as "evolutionary constraints" (see Wray, Chapter 9).

The first hypothesis that one might pose about a clade that has failed to radiate could invoke lack of ecological opportunity, but it is not clear how one would test this idea.[7] A way of doing so might involve estimating selection on an adaptive landscape (Fear and Price 1998; Schluter 2000; Arnold et al. 2001). The existence of unutilized adaptive peaks might suggest that a species had the opportunity to diversify and occupy those peaks. Of course, the existence of multiple adaptive peaks on a landscape does not guarantee that selection would push a clade to diversify to produce species occupying all of these peaks: speciation must occur, and the landscape itself will change when other species are present. Research of this type has rarely been conducted, the most thorough being studies on Darwin's finches (Schluter and Grant 1984; Schluter 2000; see also Case 1979). Development of these sorts of ideas is needed to make ecological opportunity a fully operational and predictive concept.

As a result, currently ecological opportunity is only recognizable after the fact, as a plausible and often surely correct explanation for why a clade radiated.[8] As such, the concept may have great heuristic value in understanding what causes adaptive radiation, but it may have little operational value in the absence of a radiation to predict whether radiation could occur.

Adaptive Divergence, Speciation, and Adaptive Radiation

Adaptive radiation has two components: proliferation of species (speciation) and divergence of species into different ecological niches (Losos 2009; see Harrison, Chapter 13). Two important questions concern: (1) whether any process other than natural selection could produce adaptive divergence and (2) whether speciation and adaptation are causally connected.

Divergence of species to utilize different aspects of the environment could occur in two ways, either with genetic drift playing a large role or by divergent natural selection. Although drift by itself would not be expected to lead

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[7] In this regard, one might suggest that the concept of ecological opportunity suffers from the same problems as the empty niche concept (Chase and Leibold 2003). Both empty niches and ecological opportunity are difficult to identify in the absence of species that fill or take advantage of them. Moreover, one might question whether resources are ever truly unutilized. How often, for example, is some type of food resource not eaten by any organism? If nothing else, they are a resource for decomposers, which is the reason for the wording of the definitions of ecological opportunity presented earlier.

[8] Ecological opportunity is also an explanation for why some species exhibit exceptionally broad ecological and phenotypic diversity, which is arguably the first step in adaptive radiation (Parent and Crespi 2009).

to adaptive change, in an adaptive landscape, it is possible that it could move a population off one adaptive peak and into the domain of another (the basis of Wright's 1932 famous shifting balance theory). Alternatively, drift could move a population along an adaptive ridge, from one high point in an adaptive landscape to another equally high point, assuming that the two points are connected by a ridge of equally high fitness (Schluter 2000). While these scenarios could ultimately result in the evolution of a suite of adaptively differentiated species, they have received relatively little empirical support. Rather, the standard and widely accepted view is that adaptive radiation is driven by divergent natural selection, in which species diverge as they adapt to use different parts of the environment. Most theories of adaptive radiation assume that a trade-off exists, such that enhanced adaptation to use one part of the environment comes with a concomitant cost of decreased adaptation to another part of the environment. Evidence for such trade-offs is strongly implied by work on polymorphisms and local adaptation (Schluter 2000), although the specific traits involved are often unknown (see Agrawal et al., Chapter 10).

With regard to the second question, speciation and adaptive divergence could be related in a number of ways:

1. Allopatric speciation could occur with adaptive divergence.
2. Allopatric speciation could occur without adaptive divergence, followed by adaptive divergence when species secondarily establish sympatry.
3. Some degree of adaptive divergence and evolution of reproductive isolation could occur in allopatry, followed by enhanced adaptive divergence and completion of the speciation process in sympatry (if not completed in allopatry).
4. Speciation could occur in sympatry accompanied by adaptive divergence. With respect to adaptive radiation, adaptive divergence is usually invoked as an integral part of the speciation process, though in theory, sympatric speciation could occur in non-adaptive ways (e.g., by polyploidy), followed by adaptive divergence, which would occur as in the first scenario in this list.

Few workers have suggested that most or all of the adaptive divergence during adaptive radiation evolves in allopatry (option 1). Rather, sympatric divergence, either during or after speciation (options 2, 3, and 4), is the primary, though not exclusive, focus of theoretical and empirical discussion.

Sympatric speciation driven by disruptive selection is in a way the most biogeographically parsimonious explanation for the occurrence of a clade of co-occurring, ecologically differentiated species, because it does not require the invocation of one or more rounds of range contraction and expansion to permit allopatric speciation followed by current-day sympatry. Nonetheless, the possibility of sympatric speciation of this sort is highly controversial, and probably the majority of workers consider the prerequisites for it to occur to be very stringent and likely to be met by few organisms in most settings (Coyne and Orr 2004; Gavrilets 2004; Bolnick and Fitzpatrick 2007; see Harrison, Chapter 13). In a few examples, the case for adaptive radiation by sympatric speciation is strong. The most convincing is the occurrence of two clades of ecologically differentiated cichlid fishes, each one in different volcanic crater lakes in Cameroon (Schliewen et al. 1994). The monophyly of the clades (comprised of 9 and 11 species) makes *in situ* speciation far more plausible than the alternative of many colonization events followed by extinction of related forms outside the lakes (which would make the lake species monophyletic with respect to extant species). The lakes are small and homogeneous, so it is hard to imagine an allopatric phase in the speciation process, leading to the conclusion that sympatric speciation likely occurred.

Many clades of insects, some extremely species-rich, are composed of species adapted to specialize on different host plants (see Berenbaum and Schuler, Chapter 11). In many cases, multiple—sometimes many—clade members occur sympatrically. Some workers in this area consider the evolution of sympatric host-specialist species to be most readily explicable by sympatric speciation (Berlocher and Feder 2002; Drès and Mallet 2002; Abrahamson and Blair 2008). However, controversy over the theoretical likelihood of sympatric speciation also pertains to host race speciation (Coyne and Orr 2004; Gavrilets 2004; Bolnick and Fitzpatrick 2007). Futuyma (2008) argued that the empirical evidence in support of this view is not generally strong and suggests that host shifts in allopatry are a likely alternative possibility. Although the literature on these insects usually is not couched in terms of adaptive radiation (exceptions include Després and Cherif 2004; Price 2008; Roderick and Percy 2008), many host-specialist complexes surely are adaptive radiations, and if sympatric speciation is a common mode of speciation in these groups, then they may represent examples of adaptive radiation by sympatric speciation.

The extreme alternative to adaptive divergence during sympatric speciation is speciation in allopatry without adaptive ecological divergence. Subsequently, the new species become sympatric and as a result of divergent natural selection, adapt to different ecological niches (i.e., ecological character displacement). Speciation without adaptive divergence could occur if allopatric populations diverge and become reproductively isolated as a result of genetic drift or if sexual selection pressures in the two populations lead to the evolution of different mating preferences (Gittenberger 1991; Price 2008). One difficulty with these scenarios is that, if resources are limiting, ecologically undifferentiated species may compete when they become sympatric and thus, may not be able to coexist long enough for evolutionary divergence to occur (MacArthur and Levins 1967; Slatkin 1980; Gomulkiewicz and Holt 1995).

An intermediate possibility emphasizes the role that different selective environments may play in causing allopatric populations to diverge. Studies in both the laboratory and in nature clearly indicate that isolated populations experiencing different selective pressures are more likely to evolve reproductive isolation as an incidental result of adaptive differentiation (Rice and Hostert 1993; Funk et al. 2006; Funk and Nosil 2008) (Figure 15.6). Consequently, speciation is more likely to occur, or at least be initiated, by populations experiencing different selective pressures. Moreover, if such populations become sympatric, the evolved differences in ecology increase the possibility that the populations can coexist long enough for character displacement to occur, leading to greatly enhanced ecological differentiation that permits coexistence. This scenario corresponds to the archipelago model of adaptive radiation (Grant and Grant 2008a; Price 2008).

Because species proliferation is required for adaptive radiation to occur, taxa that are more likely to speciate may also be more likely to adaptively radiate. Thus, factors that predispose taxa to speciate, such as a mating system emphasizing female choice, may be linked to adaptive diversification (Schluter 2000; Rundell and Price 2009). In the same vein, the evolution of a trait that leads to enhanced speciation rates may be the trigger that promotes adaptive radiation in a group, if ecological opportunity is already present.

Overall, the role of speciation in adaptive radiation is poorly understood. In recent years, "ecological speciation"—the idea that divergent adaptation to different environments leads to the speciation—has attracted considerable attention (for insightful reviews, see Hendry 2009 and see Harrison, Chapter 13). There is no doubt that adaptation to different environments by allopatric populations enhances the likelihood that those populations will become reproductively isolated, and this model is a key stage in the standard model for adaptive radiation on islands. Whether or not ecological speciation in sympatry (i.e., sympatric speciation) commonly occurs and leads to adaptive radiation is an open question. Similarly, the role of nonadaptive modes of speciation, such as founder effect speciation, in adaptive radiation is also controversial (Coyne and Orr 2004; Gavrilets 2004; Futuyma 2005; Price 2008). More generally, the extent to which adaptive radiation is limited by the production of new species is unclear and thus the degree to which factors that promote speciation may be important indirect promoters of adaptation radiation remains uncertain.

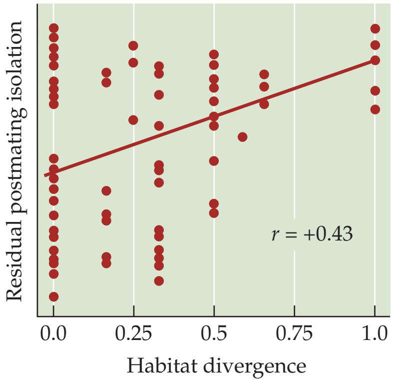

FIGURE 15.6 The Relationship between Divergent Adaptation and Reproductive Isolation The more dissimilar two species are in habitat use, the greater the degree of reproductive isolation that has evolved between them. Each point represents the degree of difference between two closely related species or populations. (Adapted from Funk et al. 2006.)

Adaptation to Different Aspects of the Environment in the Absence of Interspecific Interactions

Regardless of how speciation occurs, what ecological mechanisms drive adaptive divergence? Divergent natural selection is the underlying cause, but the question is whether the driving force behind such selection is simply adaptation to different aspects of the environment or whether interspecific interactions change the selective landscape, producing divergent selection that would not occur in the absence of the interacting species (Schluter 2000).[9]

It is easy to envision how two allopatric populations experiencing different environments would evolve different adaptations. Moreover, because the environment and hence, the adaptive landscape is rarely identical in different places, it is possible that two adaptive peaks that are separated by an adaptive valley in one location may be connected by an adaptive ridge in another. Suppose a population on one island occupied the lower of two adaptive peaks, which were separated by an adaptive valley, so that the higher peak was not attainable. If members of that population colonized a second island on which the peaks were connected by an adaptive ridge, then the population would adapt to the higher peak. Subsequently, if members of the second population colonized the first island, they would occur on the higher peak, producing sympatry of the species on different peaks (Figure 15.7).

In theory, this sort of scenario, in which adaptive divergence occurs entirely in allopatry, could lead to adaptive radiation, producing species adapted to many different aspects of the environment. Most views of adaptive radiation do not take such an extreme view, though proponents of the role of interspecific interactions envision allopatric differentiation as the initial step in divergence, setting the stage for subsequent, much more substantial divergence in sympatry that is driven by sympatric interactions (i.e., character displacement).

An alternative view is that divergent selection in sympatry can split an initially homogeneous population into distinct, reproductively isolated and

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[9] In this discussion, we consider the food an organism eats to be part of the environment. By interspecific interactions, we refer to interactions among species on the same trophic level or between the focal species and other species on higher trophic levels.

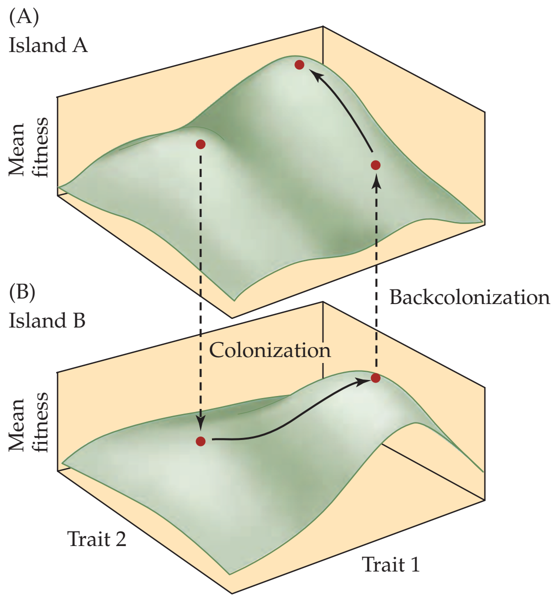

FIGURE 15.7 Peak Shifts along an Adaptive Ridge (A) The ancestral species occurs on the lower adaptive peak on Island A. Because an adaptive valley lies between the two peaks, natural selection cannot drive the population to the second peak. (B) However, on Island B, an adaptive ridge connects the ancestral position to a higher peak, and when individuals immigrate to Island B from Island A, the new population on Island B evolves a new morphology. Subsequently, the population on Island B evolves reproductive isolation. When individuals from Island B then recolonize Island A, they may evolve to the second peak on that island, leading to the coexistence of two species—one on each adaptive peak. (Adapted from Schluter 2000.)

adaptively differentiated populations. Some variants of this model envision intraspecific resource competition or interspecific interactions as the driving force, but many prominent proposals, particularly those concerning host–plant specialists (see following discussion), simply invoke adaptation to different aspects of the environment, requiring a tradeoff such that disruptive selection produces a bimodal distribution of phenotypes. As just discussed, the prerequisites for reproductive isolation to evolve in such a scenario are very strict, and controversy still exists on how likely it is to occur, even in host–plant specialized insects.

Adaptation to Different Aspects of the Environment as a Result of Interspecific Interactions

Interspecific Competition

Dating back to the seminal work by Simpson (1953), which focused primarily on vertebrates, a commonly held view is that adaptive radiation primarily results from interspecific competition for resources, leading to character displacement and adaptation to different resources (Schluter 2000; Grant and Grant 2008a). Repeated numerous times, this process leads to sympatric coexistence of species adapted to a variety of different ecological niches (i.e., an adaptive radiation).

Although character displacement was controversial in the 1970s and 1980s, a growing consensus exists that it is an important evolutionary phenomenon (Schluter 2000; Dayan and Simberloff 2005; Pfennig and Pfennig 2009). Experimental studies have confirmed that interspecific competition can lead to strong divergent selection (Schluter 1994; Schluter 2003), and the process of character displacement has been directly observed in the field in Darwin's finches (Grant and Grant 2006) (Figure 15.8) as well as in laboratory studies (e.g., Barrett and Bell 2006; Tyerman et al. 2008; Kassen 2009). It seems safe to conclude that interspecific competition-driven character displacement is a common means by which adaptive radiation occurs.

The question is, then, whether interactions other than competition can lead to adaptive radiation, and if so, whether they have been important in driving adaptive radiations throughout the history of life.

Predation, Parasitism, and Herbivory

In ecological terms, predation, parasitism, and herbivory are similar processes in that they refer to individuals of one species directly consuming members of another species (hence, we refer to all as "predators" in the following discussion). These processes could produce divergent natural selection pressures when species adapt to different predators or when species adapt in divergent ways to the same predator. Moreover, species initially preyed upon by the same predator may diverge so as not to share the same predator. Although predation may spur divergence and diversification, it also can hinder it, and the extent to which predation plays an important role in driving adaptive radiation remains poorly understood (Vamosi 2005; Langerhans 2006).

One can easily envision how species occurring in different places, with different predation regimes, would face selection to evolve different phenotypes. Several recent studies have demonstrated the importance of predation in driving such divergence. For example, both mosquitofish and damselflies exhibit differences in their behavior, habitat use, and morphology depending on which predators are present in the lakes in which they occur (McPeek et al. 1996; Stoks et al. 2003; Langerhans et al. 2007).

In sympatry, predation-driven selection may be divergent for several reasons. First, multiple ways may exist to avoid predation. For example, *Timema* walking sticks that use different host plants have diverged to enhance crypsis on the differently colored plants; manipulative experimental studies demonstrate that selection is divergent when predators are present (Nosil and Crespi 2006) (Figure 15.9). Among garter snakes, disruptive selection favors striped individuals that rapidly flee from predators and

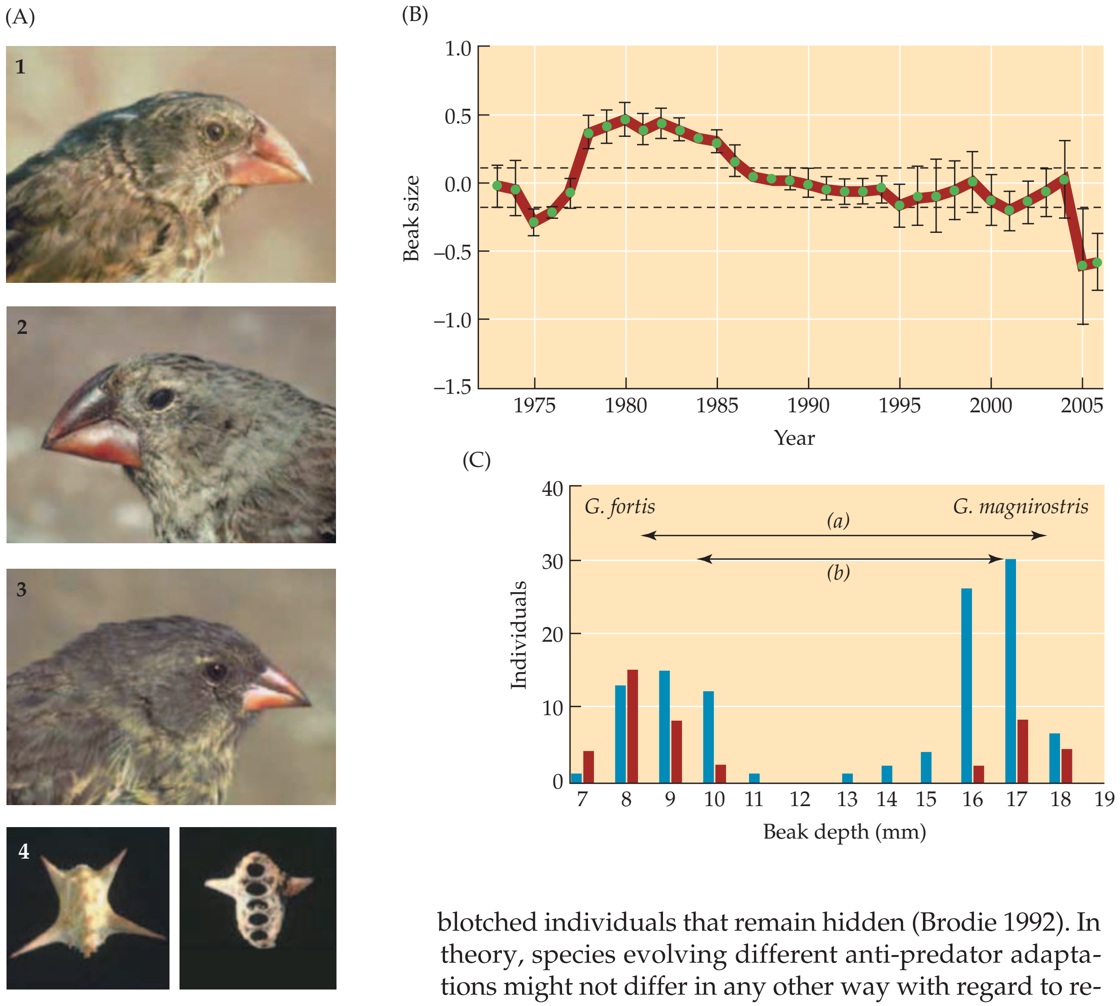

FIGURE 15.8 Character Displacement in Darwin's Finches (A) Daphne Major, in the Galápagos Islands, harbors both the large ground finch, *Geospiza magnirostris* (A2), and the medium ground finch, *Geospiza fortis* (A1, A3), the latter of which exhibits substantial variability in beak shape. Only large-beaked birds can eat large seeds, such as those from *Tribulus cistoides* (A4). (B) During the drought of 1977, when only the medium ground finch occurred on the island, small seeds were rapidly consumed and only large seeds remained. Selection strongly favored large-beaked medium ground finches (as indicated by the calculation of selection gradients, which are not shown here), and the population evolved larger beak size. Another drought occurred in 2003 and 2004; however, in the intervening years, the large ground finch had colonized Daphne Major. During this drought, the large ground finches monopolized the larger seeds. Mortality was very high in both species, and in the medium ground finch, smaller-beaked birds that could eat the few remaining small seeds were favored, and the population evolved smaller beak size, the opposite of what occurred in the absence of the large-beaked ground finch. Beak size units represent scores on the first axis of a principal components analysis of six bill measurements. (C) Thus, in the 2003–2004 drought, selection favored smaller-beaked birds in the medium ground finch and larger-beaked birds in the large ground finch, and the phenotypic distributions before the drought (indicated by blue bars) and afterwards (indicated by red bars) can be compared; as a result, differences in beak size between the two species were greater after the drought (arrow a) than before (arrow b), making this a classic example of character displacement. (A, photos from Grant and Grant 2006; B, adapted from Grant and Grant 2006; C, adapted from Grant and Grant 2008b.)

blotched individuals that remain hidden (Brodie 1992). In theory, species evolving different anti-predator adaptations might not differ in any other way with regard to resource or habitat use, in which case ecological opportunity might not be involved in adaptive divergence. However, most documented examples include correlated shifts in other ecological and behavioral aspects; the evolution of body armor, for example, has consequences for locomotion, which in turn may affect where and how an animal can forage (Bergstrom 2002; Losos et al. 2002). Consequently, in this predator-driven scenario for adaptive radiation, ecological opportunity would still be required; multiple distinct habitats or resources to which different prey species could adapt would be necessary, and these different niches could not already be preempted by other species.

Selection may also favor sympatric species to diverge in habitat use so as to avoid being preyed upon by the same predator. If prey species are preyed upon by the same predator, then under some circumstances, increased population size of one of the prey species would lead to increased population size of the predator; thus, the population size of the other prey species would decrease, as they are preyed upon by the greater number of predators. The result is that a negative relationship would exist between the population sizes of the prey species, just as would occur through interspecific competition (Holt 1977). Assuming the predator species is not able to function equally successfully in all parts of the environment, prey species may diverge to use different resources or habitats, if they are available, and thus no longer share predators. Subsequently, prey species would adapt to the different habitats or resources they were utilizing, producing the same outcome as competition-driven character displacement: an adaptive radiation driven by "competition for enemy free space" (Jeffries and Lawton 1984) or "apparent competition" (Holt 1977).

In theory, adaptive radiation also could result from predation-driven divergent selection by the means just outlined. However, we are aware of few purported cases. The diversity of some tropical butterfly clades, involving multiple mimicry complexes and a suite of other ecological and behavioral differences, might be one example (Elias et al. 2008).

Processes Driving Radiation: Conclusions

The role of interspecific competition in driving evolutionary radiation is well established and likely to be of paramount importance. Other ecological processes may be important, either directly (e.g., predation, herbivory,

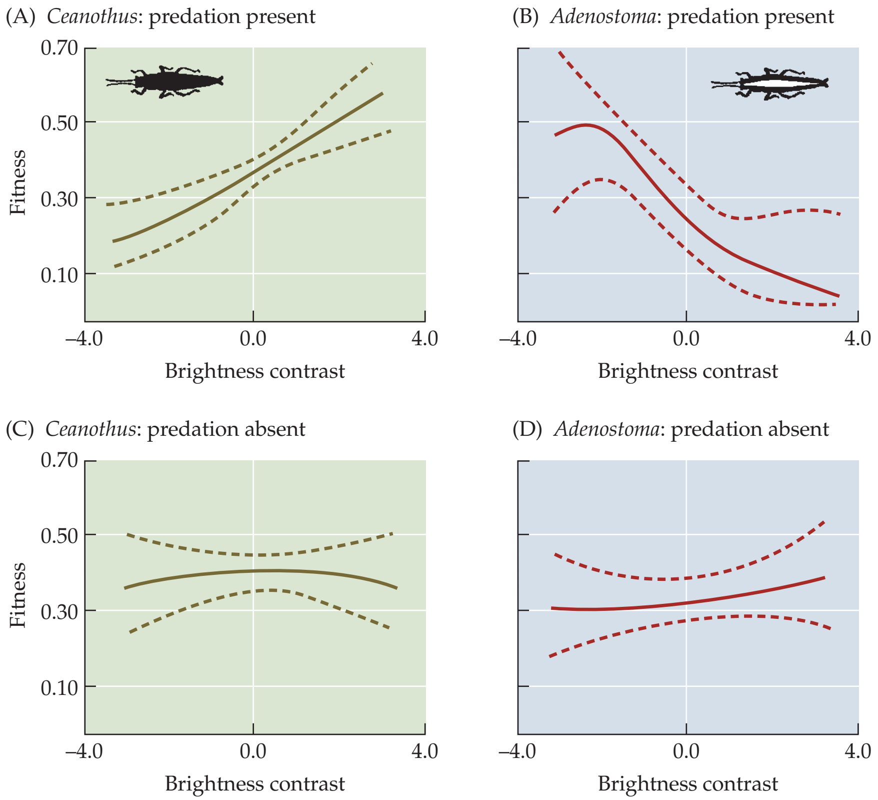

FIGURE 15.9 Selection for Background Matching in the Walking Stick, *Timema cristinae* Experimental studies of selection reveal that in the presence of avian predators, dull stripes, and bright bodies ("brightness contrast" is body brightness minus stripe brightness) are favored in the *Ceanothus* ecotype (A) and bright stripes and dull bodies in the *Adenostoma* ecotype (B). In the absence of predators, selection does not differ between insects on the two bushes (C and D). (Adapted from Nosil and Crespi 2006.)

and parasitism) or indirectly (e.g., mutualism and coevolution), by creating the opportunity for other processes to operate. However, empirical evidence demonstrating the role of other ecological processes is sparse. To some extent, this paucity of case studies, may be a result of the historical focus on competition as a driver of character displacement, but attention among both theorists and ecologists to other mechanisms has occurred for long enough now that one might expect more examples to have been documented. The lack of such examples would seem to be indicative of their limited importance relative to that of direct competition. Certainly, the evolution of mutualisms and coevolution are events that can trigger adaptive radiation. How frequently they occur is unclear.

Laboratory experiments on microbial evolution support these conclusions (see Dykhuizen, Commentary 2). Kassen (2009) reviewed the rapidly growing literature in this field and found overwhelming support for the role of interspecific competition as the primary driver of adaptive radiation. The addition of predators as an experimental treatment occasionally enhanced adaptive radiation but only when the variety of resources was limited. In situations with a wide variety of resources, the presence of predators slowed, rather than enhanced, the rate of adaptive diversification (Meyer and Kassen 2007; see also Benmayor et al. 2008). Other possible triggers for adaptive radiation, such as ecosystem engineering or the evolution of mutualisms, also rarely are important (Kassen 2009). The correspondence between the results from experimental laboratory studies and the empirical literature from nature suggests that interspecific competition is the primary driver of adaptive radiation.

Conclusions and Future Directions

Many of what we consider the classic ideas about adaptive radiation are well supported. In particular, ecological opportunity usually is the key to adaptive radiation, and interspecific competition often is the driving force behind it. Nonetheless, these are generalizations, and further work is needed to understand the relative frequency and significance of alternatives. In many cases, other possibilities, such as the role of predation in driving adaptive radiation or the extent to which radiations create their own ecological opportunity, have been little explored. Whether further work will alter the bigger picture of our understanding of adaptive radiation remains to be seen.

We also conclude that while ecological opportunity is typically necessary, it is not sufficient for adaptive radiation, as many clades seemingly in the presence of opportunity fail to radiate. Several factors likely contribute, but at present, these are too poorly understood to predict with any certainty whether adaptive radiation will occur in the presence of ecological opportunity. Why, for example, did Darwin's finches, but not mockingbirds, radiate in the Galápagos? Experimental diversification studies have come to the forefront in filling this gap; the combination of replication, strict environmental control, and fine-scale genetic characterization of lineages makes for a promising approach to dissect the nature of historical contingency in adaptive radiation (Lenski and Travisano 1994; Fukami et al. 2007; Blount et al. 2008).

While we have offered a review of the current knowledge pertaining to adaptive radiation, numerous basic questions about adaptive radiation remain unanswered, and recent conceptual and technological advances promise to lead adaptive radiation research into exciting new directions. Toward this end, we suggest that new approaches that take advantage of both conceptual and technological advances may be instrumental in moving forward understanding of adaptive radiation in years to come.

Our review has focused, for the most part, on the role of external environmental factors in shaping adaptive radiation. However, over the last several decades, evolutionary biologists have debated the role that internal constraints—manifested in limitations and directionality in the availability of phenotypic variation upon which selection can operate—play in limiting and directing evolutionary change (Gould 2002).

The role of such constraints on adaptive radiation is now being addressed in two distinctive ways. On one hand, a number of researchers have suggested that interspecific hybridization can provide enhanced variation that may be critical in allowing extensive adaptive diversification. On the other hand, the burgeoning field of genomics is now at last permitting evolutionary biologists to truly understand the relationship between genetic change and phenotypic response.

Hybridization

Several authors have recently suggested that hybridization among closely related species may play an important role in generating adaptive diversity during the early stages of adaptive radiation (Rieseberg et al. 1999; Seehausen 2004; Grant and Grant 2008a,b; Mallet 2009). Increasingly sophisticated methods are being developed to distinguish past gene flow from incomplete lineage sorting, permitting detection of historical hybridization in a phylogenetic framework (Hey and Nielsen 2004; Hey et al. 2004; Kubatko 2009), which may facilitate investigation of the contribution of hybridization to adaptive diversification. Nonetheless, directly measuring the effect of hybridization on divergence in the wild is often difficult because of the low frequency of hybridization events and the infeasibility of tracking hybrid lineages over many generations, although Grant and Grant (2008b, 2009) provide remarkable examples in Darwin's finches. However, future studies might assess the role of hybridization in adaptive radiation by testing whether radiations that exhibit historical signatures of hybridization exhibit greater adaptive diversity than radiations in which there is little evidence of hybridization.

Genomics

Thanks to the ever-decreasing cost of genome sequencing, the ability to examine the genomes of multiple members of an adaptive radiation will soon be readily available. With such information, researchers will be able to examine the extent to which genetic architecture constrains and directs the pathways by which adaptive diversification has occurred. Combined with studies of natural selection in the field, we soon will have the ability to fully integrate genetics and the study of natural selection to understand how and why adaptive radiation has occurred. Experimental studies of this sort have already been conducted (e.g., microbial laboratory experiments: Bantinaki et al. 2007 and Spencer et al. 2007; sticklebacks: Barrett et al. 2008) and no doubt will soon become commonplace. The next 10–20 years should prove extremely enlightening as the integration of genomic and selection studies, in a phylogenetic context, ushers in a golden age for the study of adaptive radiation.

The Impact of Adaptive Radiation on Communities and Ecosystems

Finally, virtually all research on adaptive radiation has investigated the influence of ecological factors on adaptive diversification, but until recently, few have asked how the process of adaptive radiation may alter the structure of communities and ecosystems. Adaptive radiation typically involves a dramatic change in the ecological diversity of a lineage, usually within a local setting. Diversification may influence community interactions, alter food webs, and ultimately affect nutrient and energy flow in ecosystems, and radiations have been implicated in major ecological changes in Earth's history (e.g., the rise and proliferation of autotrophs changing the atmospheric oxygen concentration roughly 2 billion years ago). However, only recently has research specifically sought to quantify the influence of evolutionary diversification on community structure and ecosystem function (Loueille and Loreau 2005, 2006; Harmon et al. 2009; Ingram et al. 2009). Continued research in this direction may result in a richer understanding of the complex and interactive relationship between ecological and evolutionary diversity.

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