Adaptive radiation is one of the most important outcomes of the process of evolution, and islands are places where it is best observed. The term itself was first used by Osborn in 1902 in describing parallel adaptations and convergence of species groups on different land masses. Since then, the phenomenon has been widely recognized and defined in multiple ways to emphasize the contribution of key features thought to underlie the phenomenon, including adaptive change, speciation within a monophyletic lineage, and time. Dolph Schluter, a prominent researcher, defines it as “the evolution of ecological diversity within a rapidly multiplying lineage.”

There are radiations that are not adaptive. These are mostly caused by changes in topography that, instead of opening up new habitats, have served simply to isolate a previously more widespread species. Island radiations are likely to include adaptive as well as non-adaptive evolutionary elements. In this article, the focus is on adaptive evolutionary radiations.

**Factors Underlying Adaptive Radiation**

The most widely recognized “trigger” for adaptive radiation is the opening up of ecological space. This may occur following evolution of a key innovation or when climatological or geological changes lead to the appearance of novel environments. Islands of all sorts are examples of these kinds of environments, which contribute to the emergence of novel evolutionary changes.

**Key Innovations**

Key innovations are, for example, adjustments in morphology/physiology that are essential to the origin of new major groups, or features that are necessary, but not sufficient, for a subsequent radiation. It appears that the new trait can enhance the efficiency with which a resource is utilized and hence can allow species to enter a “new” adaptive zone in which diversification occurs. For example, with the origin of powered flight in birds, new feeding strategies, life history patterns, and habitats became available. Likewise, the origin of jaws in vertebrates allowed rapid diversification of predatory lineages. However, key innovations only set the stage for changes in diversity; they do not, by themselves, cause the change.

Key innovations can occur over and over, such as heterospory in plants. They have been extensively implicated in the adaptive radiation of interacting species. For example, symbioses can be an “evolutionary innovation,” allowing the abrupt appearance of evolutionary novelty, 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. The development of toxicity in plants (which can allow them to “escape” the predatory pressure of insects) can lead to a subsequent development of tolerance to the toxin in insects, allowing the insects to radiate onto the plants. Paul Ehrlich and Peter Raven envisioned this as a step-like process in which the major radiations of herbivorous insects and plants have arisen as a consequence of repeated openings of novel adaptive zones that each has presented to the other over evolutionary history. This idea, termed the “escalation/diversification” hypothesis,
has been supported by studies of phytophagous beetles. A recent study in butterflies has shown that a key innovation (evolution of the NSP glucosinolate detoxification gene) has allowed butterflies (Pierinae) to radiate onto plants (Brassicales) that had temporarily escaped herbivory from the caterpillars.

**Novel Environments**

When a new habitat forms close to a source, it is generally colonized by propagules from the adjacent mainland. However, if the new habitat is isolated, as in the case of the formation of islands in the ocean, then colonization may be very slow, to the extent that evolution may contribute to the formation of new species more rapidly than does colonization. It is under such conditions that some of the most remarkable adaptive radiations have occurred (Fig. 1). Geological history is punctuated with episodes of extinction, presumably induced by catastrophic environmental changes, with each extinction episode setting the stage for the subsequent adaptive radiation of new (related or unrelated) groups. Environmental change has, for example, been implicated in Phanerozoic revolutions and the repeated radiations of ammonoids throughout the geological record, in which each radiation appears to have originated from a few taxa that went on to give rise to morphologically diverse lineages. Some of the best examples of recent, or ongoing, adaptive radiations come from isolated islands, including oceanic archipelagoes, continental lakes, and mountaintops. Galápagos island finches, Hawaiian honeycreepers, Madagascar lemurs, and African cichlids are frequently cited as some of the best examples of adaptive radiation. The finches are well known because of their historical importance, being a focus of discussion by Darwin in the *Origin of Species*. Thirteen species of Galápagos finch (Geospizinae, Emberizidae) have diversified on the Galápagos Islands, with each filling a different niche on different islands. The clear similarity among species in this radiation, coupled with the dietary-associated modifications in beak morphologies, played a key role in

**FIGURE 1** Adaptive radiation of weevils, genus Cratopus (Coleoptera, Curculionoidea), on the small island of La Réunion. The southwestern Indian Ocean is a hotspot of terrestrial diversity and endemism. The genus Cratopus has undergone intense diversification within the islands of the Mascarenes, including a total of 91 species, of which 43 are present on La Réunion (21 endemic), 36 on Mauritius (28 endemic), and five on Rodrigues (all endemic). Research is currently under way to elucidate the nature of diversification in this group. Photographs by Ben Warren, Christophe Thébaud, Dominique Strasberg, and Antoine Franck, with permission.

**FIGURE 2.** Adaptive radiation of Hawaiian lobelioid plants. The very large and spectacular radiation of plants (125 species in six genera) appears to have occurred together with that of its pollinators, the Hawaiian honeycreepers. Species shown are (A) Trematolobelia macrostachys, Poamoho Trail, Ko‘olau Mountains, O‘ahu; (B) Clermontia samuelii, Upper Hana rain forest, East Maui. See also Figs. 3, 4. All photographs by Gerald D. Carr, with permission, except where noted.
the development of Darwin’s theory of evolution through natural selection. Research on the finches has continued to illuminate evolutionary principles through the work of Rosemary and Peter Grant.

Hawaiian honeycreepers (Drepaniinae, Emberizidae) also originated from a finchlike ancestor and diversified into approximately 51 species in three tribes, with extraordinary morphological and ecological diversity. However, a large proportion of these species (about 35) are now extinct.

Isolation is a relative phenomenon. Accordingly, islands that are isolated for mammals and lizards are less so for many insects, with mammal radiations known in less isolated islands such as the Philippines (radiation of Old World mice/rats, Murinae), and lizards in the Caribbean (Anolis diversification in the Greater Antilles); prior to human transportation, few vertebrates, except for birds and an occasional bat, succeeded in colonizing more remote islands. However, the most remote islands of the central Pacific are well known for some of the most spectacular radiations of arthropods and plants.

**Examples of Insular Radiation**

Some adaptive radiations are perhaps best known because of the number and rate of species that have been produced. One of the most spectacular in this regard is the Hawaiian Drosophilidae, with an estimated 1000 species divided into two major lineages (Hawaiian Drosophila and Scaptomyza). However, the cricket genus Laupala has been documented as having the highest rate of speciation so far recorded in arthropods, with 4.17 species per million years, supporting the argument that divergence in courtship or sexual behavior can drive rapid speciation in animals. Very rapid rates of speciation have also been reported for the African cichlid fish, with an estimated 2.02–2.09 species being formed per million years in Lake Malawi and Lake Victoria. Here again, sexual selection is implicated in the diversification of the group. A recent study, which awaits explanation, is that of Hawaiian bees (Hylaeus, Colletidae), which indicates that the 60 species known to occur on the islands originated and radiated on the island of Hawaii less than 700,000 years ago.

Most island adaptive radiations occur within an archipelago setting, and the argument is often made that different islands are necessary to provide sufficient isolation for adaptive radiation to take place. Interesting in this regard is a radiation of small flightless weevils in the genus Micrales (Coleoptera: Curculionidae: Cryptorhynchinae) on the single small island of Rapa in the southern Australs of French Polynesia. Rapa is home to almost half of the 140 species that occur across the western Pacific and Australia. Here, the beetles collectively feed on 24 genera of native plants and show varying degrees of host specificity, thus utilizing almost all genera of native plants found on Rapa.

Some radiations have been studied because they are readily accessible to scrutiny of the process of adaptive
radiation, in part because they have occurred very recently. In this context, research of Dolph Schluter has focused on stickleback fish of the deglaciated lakes of coastal British Columbia, Canada. These lakes harbor a number of sibling species of fish, and repeated co-occurrence of pairs of species has been attributed to novel ecological opportunities provided by deglaciation and recolonization. In particular, the threespine stickleback, *Gasterosteus aculeatus*, is a species complex that has diversified in each lake such that no more than two species occur in any one lake. Interestingly, it appears that pairs of species in different lakes have evolved independently of other pairs, and species have diverged as a result of parallel episodes of selection for alternate feeding environments. Research in this system has highlighted the role of divergent natural selection as a mechanism underlying adaptive radiation.

Among plants, the largest known radiation is that of the Hawaiian lobelioids (*Brighamia*, *Cyanea*, *Clermontia*, *Delissia*, *Lobelia*, and *Trematolobelia*—Campanulaceae), with the more than 100 species now thought to have arisen from a single colonization event (Figs. 2–4). The radiation exhibits extraordinary diversity in vegetative and flower morphology, with species inhabiting a huge array of habitats. The diversity is considered to have arisen in concert with that of the Hawaiian honeycreepers, the lobelioids displaying a suite of morphological characteristics associated with bird pollination, including deep, tubular, long-lived inflorescences, with an abundance of nectar and no odor. Another spectacular example of adaptive radiation in plants is the Hawaiian silversword alliance, *Argyroserpium*, *Dubautia*, *Wilkesia* (Asteraceae–Madiinae), in which 28 species are known that display a huge diversity in life form, from trees to shrubs, mats, rosettes, cushions, and vines, occurring across habitats from rain forests and bogs to desert-like settings. An analogous radiation of 23 species in the genus *Argyranthemum* (Asteraceae–Anthemideae) has occurred in the Macaronesian islands, although the largest radiation of plants in the Canaries is that of the succulent, rosette-forming species of the genus *Aeonium* (Crassulaceae).

### Predisposition to Adaptive Radiation

Are certain taxa predisposed to adaptive radiation? Some have suggested that plant-associated insects are constrained by their narrow host range, which prevents adaptive diversification. However, this argument is not well supported, as multiple insects with specialized host affinities have succeeded in colonizing remote islands and have also undergone some of the most spectacular adaptive radiations. Based on the available information, there is no a priori means of predicting whether or not a species will undergo adaptive radiation upon being provided an ecological opportunity that it can exploit.

At the same time, some lineages do show multiple independent episodes of adaptive radiation; for example, Hawaiian silverswords have a parallel sister radiation of California tarweeds, and one sister group, the...
shrubby tarweeds (*Deinandra*), has undergone adaptive radiation on the California Channel Islands (Fig. 5). Hawaiian long-jawed spiders (genus *Tetragnatha*) have undergone independent radiations on different archipelagoes of the Pacific, presumably because they are adept at overwater dispersal and readily adapt to insular environments.

In general, although there may be a substantial random element to colonization, successful colonization of very isolated locations requires high dispersal abilities, so representation of taxa within biotas in isolated areas will be skewed toward those with high dispersal abilities. However, subsequent establishment of the initial colonists on remote islands is frequently associated with a dramatic loss of dispersal ability and/or attainment of a more specialized habitat. Indeed, loss of dispersal ability is implicated as a key factor in allowing diversification to proceed.

**PROCESS OF ADAPTIVE RADIATION**

**Ecological Release**

Ecological release has been inferred to occur at the outset of adaptive radiation. This sort of release is the expansion of range, habitat, and/or resource usage by an organism when it reaches a community from which competitors, predators, and/or parasites may be lacking. Indeed, regular cycles of ecological and distributional expansion following colonization of islands are well known and have been documented in a number of groups, with some showing subsequent shifts toward specialization, as part of the phenomenon of "taxon cycles."

**Adaptive Plasticity**

Behavioral and ecological plasticity have recently been implicated as playing a key role in adaptive radiation. Although initially thought to impede adaptive diversification because it allows a single taxon to exploit a broad environmental range without requiring evolutionary shifts, recent work by Mary-Jane West Eberhard indicates that adaptive plasticity (including behavior) can promote evolutionary shifts, in particular when the environment is variable. Accordingly, plasticity in Caribbean *Anolis* lizards may allow species to occupy new habitats in which they otherwise might not survive. Once in these habitats, selection may act to accentuate attributes that allowed them to live in this habitat. Recent studies of threespine stickleback, in which ancestral oceanic species have changed little since colonization and diversification of freshwater species, have lent support to the importance of behavioral plasticity in allowing adaptive radiation to proceed. An interesting example of how natural selection can promote plasticity, potentially leading to species radiation, is found in pitohui birds in New Guinea (Fig. 6).

**Speciation in Adaptive Radiation**

A key feature of adaptive radiation is rapid speciation coupled with phenotypic diversification. This introduces an interesting paradox in that adaptive radiations are simultaneously characterized by minimal genetic diversity (very small numbers of individuals involved in the initial colonization) and very high morphological/ecological/behavioral diversity. Given the circumstances, what are the processes that have been implicated in allowing adaptive radiation to occur?

**Founder Events**

A founder event occurs when a new population is composed of only a few colonists, inevitably carrying only a small sample of the genetic diversity of the parent population. This small population size means that the colony may have reduced genetic variation and a non-random sample of the genes relative to the original population. Many studies have suggested that founder events play a role in adaptive radiation, as taxa within a radiation are generally
characterized by small population sizes with ample opportunity for isolation. This could potentially lead to a cascade of genetic changes leading to evolutionary differentiation, an idea first formulated in the “genetic revolution” model, which posits that the reduced levels of heterozygosity following founder events affect the nature of co-adapted gene complexes. However, the precise role of founder events remains unclear: During the bottleneck, (1) a large proportion of alleles is lost, and few new mutations can occur with the population at small size; (2) genetic change will occur through drift, but the effect becomes weaker as the population starts to grow. As a result of these opposing forces, the number of beneficial mutations fixed per generation will change little because of the bottleneck. However, subsequent to a genetic bottleneck, selection can preserve alleles that are initially rare and that would otherwise tend to be lost through stochastic events. Founder events have been implicated in the adaptive radiation of such large groups as Hawaiian Drosophila and other insects, but there is little empirical evidence to support their role in species formation among vertebrates.

Divergent Natural Selection

Although adaptive radiation is generally associated with reduced competition, the process through which species are formed through adaptive shifts is generally considered to require competition between similar taxa. The ecological theory of adaptive radiation suggests that speciation and the evolution of morphological and ecological differences are caused by divergent natural selection resulting from interspecific competition coupled with environmental differences. Recent studies with walking stick insects and bacteria have suggested that predation may operate with (or instead of) competition to allow divergent natural selection.

Hybridization and Gene Flow

A traditional argument has been that gene flow among diverging populations, or hybridization between incipient species, acts to slow the process of diversification. However, recent research suggests that divergence between lineages can be increased through moderate levels of gene flow, a phenomenon termed “collective evolution.” Likewise, interspecific hybridization may be a possible source of additional genetic variation within species, increasing the size of the gene pool on which selection may act.

Sexual Selection

Sexual selection has been linked to the diversification of species within some of the most rapid adaptive radiations. In particular, although ecological diversification still plays a role, it appears that sexual selection may drive species proliferation in African haplochromine cichlids, Hawaiian Drosophila flies, Laupala crickets, and Australasian birds of paradise. In each case, female choice is implicated in driving speciation: Males (rather than females) exhibit striking colors (in the case of the cichlids), demonstrate complex mating systems that involve modifications of the mouthparts, wings, and/or forelegs with associated elaborate behaviors and leks which are visited by females (in the flies), and have distinct courtship songs (in the crickets). 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.

COMMUNITY ASSEMBLY

Colonization of an island is generally dictated by the interplay between colonization of species from the same niche in another region (e.g., on a mainland source or another island) or, in cases where isolation means that the
number of available colonists are insufficient to fill a community, by adaptive shifts from one niche to allow a taxon to exploit a new niche. Accordingly, during the course of adaptive radiation, speciation appears to play a role similar to that of immigration—although over an extended time period—in adding species to a community.

One striking aspect of adaptive radiation is the role of convergent evolution in similar habitats, and the associated parallel evolution of similar ecological forms, resulting in the production of strikingly predictable communities during the course of diversification. Some of the best examples here are the Anolis lizards of the Caribbean, where studies by Jonathan Losos and colleagues have shown that on the islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico) multiple species co-occur. Each species can be recognized as an “ecomorph,” occupying a characteristic microhabitat (e.g., tree twigs, grass, tree trunks) with corresponding morphological and behavioral attributes named for the part of the habitat they occupy. Most remarkably, similar sets of ecomorphs are found on each island and have generally arisen through convergent evolution on each island, showing that similar communities on different islands evolved independently. Studies have now demonstrated similar patterns of multiple convergences and independent evolution of similar sets of ecomorphs among multiple island settings—for example, spiders in the Hawaiian Islands, cichlid fishes of the African Rift lakes, and Madagascar and Asian ranid frogs.

The phenomenon of repeated evolution of similar forms among species undergoing adaptive radiation has led to research on the molecular basis of such apparently complex changes. Increasingly, these studies are indicating that rather small developmental shifts may lead to large shifts in morphology (Fig. 7). Accordingly, very minor developmental shifts may allow some very striking morphological and ecological shifts, which can readily be lost or gained.

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**FURTHER READING**


**FIGURE 7** Diversity of scarab beetle “horns,” used as weapons in males for access to mates. Dung beetles (Scarabaeinae) and rhinoceroses beetles (Dynastinae) are both common inhabitants of islands, and the dung pats that the beetles use can themselves be considered ephemeral islands of nutrients. Sample taxa illustrated are (A) *Dynastes hercules* (Dynastinae) from the New World tropics, including different subspecies on the islands of the Lesser Antilles; (B) representative of the genus *Golofa* (G. porterii) (Dynastinae), a neotropical lineage known for its “Mesoamerican mountaintop” pattern of biogeography; (C) *Allomyrina dichotoma* (Dynastinae) from the Old World tropics, including Japan, Taiwan, and associated islands; (D) *Proagoderus tersidorsi* (Scarabaeinae) from South Africa; (E) *Onthophagus nigriventris* (Scarabaeidae: Scarabaeinae) from the East Africa highlands, and now in Australia and Hawaii. The huge diversity of horns appears to result from subtle changes in the relative activities of different developmental pathways. Photograph montage by Doug Emlen, with permission.


**ALEUTIAN ISLANDS**

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