



The stages of vertebrate evolutionary radiation

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Evolutionists and ecologists are motivated to understand the forces that generate and maintain biological diversity. In turn, attention has focused on the relative roles of natural and sexual selection in vertebrate groups that are considered to be exemplars of evolutionary radiation. Here, we argue that recent phylogenetic and population genetic evidence shows that seemingly different vertebrate radiations follow similar evolutionary trajectories. Groups diverge along axes of habitat, trophic morphology and communication, often in that order. Notably, clades proceed to different stages of the radiation process, with the endpoint being correlated with species richness. Divergence along axes one and two (habitat and trophic morphology, respectively) is likely to follow ecological selection models; diversification along axis three (communication) probably proceeds according to sexual selection models. We speculate that a paucity of genetic variation for means of signaling that are independent of fitness traits might be the most important constraint limiting the diversification of vertebrate groups. The stages of evolutionary radiation discussed here do not apply to all organisms, but might represent a common trend.

Classic examples of vertebrate adaptive radiation, including North American postglacial fishes, African cichlids, coral reef-dwelling parrotfish, Caribbean anoline lizards and Darwin's finches, have captivated evolutionary biologists for decades. These examples provide tangible evidence of phenotypic divergence and the operation of natural and sexual selection. Recent progress in molecular phylogenetics and population genetics has yielded insight into the cladogenic pattern and genetic architecture of evolutionary radiation. Here, we aim to present a general model of the process based on this research. Groups diverge along axes of habitat, trophic morphology and communication (often in that order), which we use to define stages in the process of evolutionary radiation. Variations on this theme can be observed in a variety of vertebrate clades; however, this pattern is not universal. In certain cases, stages are collapsed, or occur in a different sequence. In our view, these exceptions do not detract from the generality of the model. Rather, they serve to identify constraints that might limit the extent of diversification.

The ideas that we propose are simplistic and one-sided. In gathering the data to support our hypothesis, we compare aquatic and terrestrial radiations, radiations that occur in the tropics and in the postglacial north, and radiations between freshwater and marine fishes (Table 1). We argue that the stages of most radiations occur because of some form of selection – natural and/or sexual – and downplay extrinsic factors. It is not our intention to suggest that extrinsic factors have been unimportant. In fact, every radiation we discuss has been shaped by external conditions (e.g. low lake fluctuations in Africa, glaciation in North America, El Niño events in the Galápagos, island size in the Caribbean, and changes in circumtropical ocean currents). Extrinsic factors have probably set the stage for these radiations, but cannot explain the deterministic patterns we see.

Our goal is to suggest a core similarity among seemingly different evolutionary radiations. The exemplars we feature are clearly not identical, neither in the number of species produced, nor in the time it has taken to achieve present-day species richness. The concept of 'radiations in stages' helps to explain these differences, and focuses attention on constraints acting in each system. This comparative perspective turns the usual question of 'why are there so many cichlids?' on its head and instead asks 'why aren't there more finches or sticklebacks?'

A model of vertebrate evolutionary radiation

We present a general framework of vertebrate evolutionary radiation (Fig. 1). In its most idealized form, radiation comprises three stages in which divergent selection drives the diversification of specific phenotypes. First, lineages diverge along the axis of habitat utilization. Next, secondary morphological specializations related to trophic resource acquisition evolve within habitats. Finally, certain groups diversify along the axis of sensory communication. Speciation events in stages one (habitat) and two (trophic morphology) probably follow the rules of ecological selection models. Lineage diversification in stage three (communication) probably occurs according to sexual selection models (Box 1). Competition for resources and/or mates drives the pattern of radiation in stages (Box 2). We do not mean to suggest that various competitive forces (e.g. ecological selection) operate exclusively at discrete stages. Rather, as illustrated in Fig. 1 and discussed below, aspects of habitat utilization, morphology and communication evolve throughout the history of a

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Table 1. Comparison of evolutionary radiations featured in this review

Radiation	Age (years)	No. of species	Habitat
Malawi cichlids	500 000	>500 per lake	Tropical, lacustrine
Sticklebacks	10 000	2/lake	Temperate, lacustrine
Parrotfish	40 million	100	Tropical, marine
Anoles	30 million	2–6 per island	Tropical, terrestrial
Finches	3 million	14 in Galápagos	Tropical, terrestrial

clade. Nonetheless, our framework does imply that different selective axes are of primary importance during sequential stages of the radiation process.

Stage one: divergence in habitat

Divergence based on preferred habitat has played an important role in the early stages of many vertebrate radiations. Among temperate freshwater fish, the evolution of macrohabitat specialists is pervasive [1]. Within sticklebacks, the divergence of benthic (bottom) and limnetic (water column) morphs has occurred independently in multiple postglacial lakes [2–4]. Between lakes, independently derived macrohabitat specialists tend to share similar morphological characters such as body shape, gape width, gill raker length and number [5].

A basal split in macrohabitat is also common in tropical lacustrine fish. The radiation of Lake Malawi cichlids is characterized by an early divergence between sand- and rock-dwelling lineages [6,7], each containing >200 species. Similar to sticklebacks, a large suite of morphological and behavioral characters can be used to distinguish members of each group, including body size and shape, dietary preferences, chromatophore patterning, reproductive behavior and trophic morphology. These eco-morphological features are also implicated in the

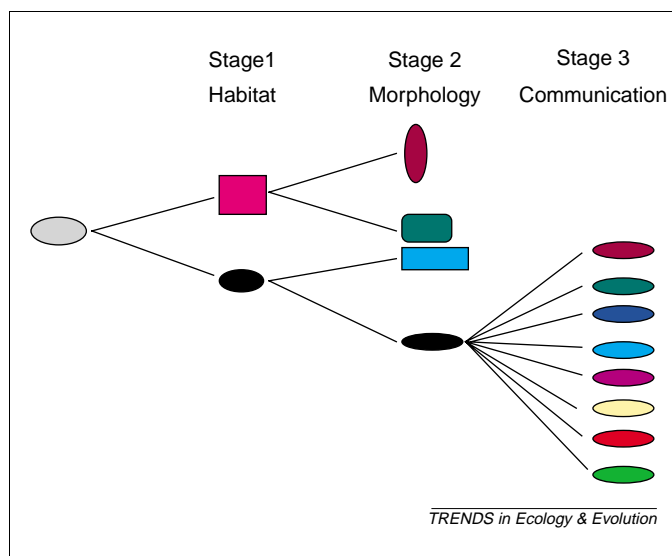


Fig. 1. Generalized framework of the radiation-in-stages pattern. Lineages (icons) diverge first along the axis of macrohabitat (stage one), followed in most cases by the evolution of trophic specialists within habitats (stage two, morphology). Finally, certain lineages exhibit bursts of species diversification associated with variance in signaling phenotypes (stage three, communication). Differently shaped icons represent phenotypic variation in morphology (e.g. body size or jaw shape) and differently colored icons represent variance in signaling phenotypes (e.g. color or song) that accompany lineage splitting at each stage.

<http://tree.trends.com>

Box 1. Relevant models of speciation

Several recent speciation models are germane to the pattern of evolutionary radiation that we describe. These can be grouped into two classes based on the nature of the selective force that drives diversification: ecological selection [a] and sexual selection [b]. Ecological and sexual selection models share two common features. Both models assume that: (1) disruptive selection (natural and/or sexual) promotes the divergence of two or more groups; and (2) mating is nonrandom.

In ecological models [c,d], reproductive isolation occurs when disruptive natural selection on a fitness-determining trait (e.g. size) is coupled with assortative mating based either on this fitness trait or some marker. This process is predicated on the association (genetic or gametic) between fitness, marker and preference characters. Divergence is accelerated if the number of genes affecting fitness is greater than that controlling differences in the signal and choice.

In contrast to models that rely on ecological competition, sexual selection models explain divergence through competition for mating opportunities [e,f]. For example, males vary in some secondary sexual character that experiences both natural (usually stabilizing) and sexual (disruptive) selection and which might or might not be an indicator of male quality. Female preference for the male character is selectively neutral (or incurs a slight cost to the female) and varies within the population. With time, a genetic correlation between male phenotypes and female preferences develop. Divergence occurs in the absence of ecological selection and is facilitated by an increase in female discrimination among males or a decrease in the cost of male ornamentation.

Under ecological selection models, phenotypic distributions will be at or near optimal and associations between ecological fitness traits and marker characters are expected to be strong. Under sexual selection models where sexual dimorphism is common, male phenotypic distributions can be shifted significantly away from their optimum as produced solely by natural selection and no correlation between ecological traits and signaling phenotypes is necessary.

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divergence of tilapiine lineages within smaller crater lakes of East Africa [8,9].

A similar divergence among macrohabitat specialists is observed in circumtropically distributed marine parrotfish (Scaridae) [10]. Approximately 40 million years ago, the ancestral parrotfish lineage diverged to form ‘reef’ and ‘seagrass’ clades. Remarkably, this split in habitat might have occurred in the absence of physical barriers to gene flow. Regional population structure is minimal among these broadcast spawners [11], and reef and seagrass habitats co-occur to such a degree that juvenile reef species mature in seagrass beds [12]. Nonetheless, ecological forces are implicated strongly in the early divergence of scarids.

Box 2. Competition drives the pattern of radiation in stages

It is probable that competition for space and trophic resources explains divergence along the first two axes of the radiation-in-stages pattern. Evidence is discussed in multiple sources [a,b] and bolstered by documented cases of convergent/parallel evolution. Examples include independent evolution of the benthic-limnetic split in sticklebacks [c], replicated origin of anole ecotypes on different Caribbean islands [d], convergence in jaw morphology among cichlids in different African lakes [e], and independent evolution of scraping and excavating feeding modes in reef-dwelling parrotfish [f].

There is evidence for a third stage of explosive diversification in two clades, cichlids and parrotfish. Cladogenic events in stage three (Fig. 1 and main text) (diversification in communication) are associated with organismal variation in sensory cues (i.e. color) and breeding or social behavior (i.e. territoriality). This suggests that sexual selection drives diversification along axis three and is responsible for species richness in certain vertebrate radiations. Evidence of competition for mates and choice based on signaling phenotypes is known in both cichlids [g,h] and parrotfish [i,j].

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Habitat divergence is also common in terrestrial vertebrates. Robert Perkins recognized this nearly a century ago with his study of Hawaiian honeycreepers [13]. He suggested that lineage splitting began in allopatry in response to local ecological pressures, but accelerated greatly following secondary contact. Lack [14] thought that Galápagos finches evolved in a similar manner with 'ground' and 'tree' clades diverging early in the radiation. Molecular phylogenies [15,16] support this hypothesis.

An early ecological separation of habitat specialists has occurred repeatedly among Caribbean anoline lizards. Each island of the Greater Antilles (i.e. Cuba, Hispaniola, Jamaica and Puerto Rico) supports an assemblage of *Anolis* spp. whose members differ in habitat use. A phylogenetic comparison of adaptive characteristics and mitochondrial DNA sequence variation rejected the hypothesis that ecomorphs,

which cluster in morphological space, are monophyletic in origin [17]. Instead, as many as six separate ecomorphs have evolved repeatedly on each of the four islands. This deterministic pattern of evolution in *Anolis* highlights the important role that the divergence of habitat utilization plays in the early stages of vertebrate adaptive radiations.

Stage two: divergence in trophic morphology

Secondary divergence in morphological traits is an apparent feature of certain vertebrate radiations. This is perhaps exemplified best by East African cichlids, which have evolved numerous trophic adaptations for food acquisition within each of the rock and sand habitats. Feeding guilds include piscivorous pursuit hunters, lie-in-wait predators, algal scrapers, molluscivores, zooplanktivores, and fin and eye biters [18]. Within the rock-dwelling clade of Lake Malawi, secondary morphological divergence gave rise to proto-genera characterized by differences in feeding behavior and the trophic apparatus [19].

Parrotfish in the reef habitat have diverged into lineages that either scrape or excavate algae from coral and rock surfaces [10]. These differences in trophic utilization are associated with concomitant changes in the craniofacial skeleton and musculature [20,21], feeding rate and kinematics [22]. By contrast, the seagrass lineage of parrotfish does not exhibit secondary divergence in morphological features; nearly all species are browsers (but see [23] for the interesting case of the genus *Sparisoma*).

Ground-dwelling Darwin's finches display differences in beak shape, associated with variance in foraging proficiency on hard versus soft seeds [24]. Variation in trophic morphology also distinguishes tree-dwelling finch species that occupy different microhabitats. Similarly, *Anolis* lizards exhibit morphological divergence within primary ecotype classes [25]. On the islands of Hispaniola and Cuba, members of the trunk-crown and twig ecotypes vary in body size and prey type.

Stage three: diversification in communication

Phylogenies of cichlids and parrotfish suggest that bursts of signaling evolution, usually involving male secondary sexual characteristics, follow bouts of divergence in habitat utilization and trophic morphology [10,19]. Notably, the explosive evolution of signaling phenotypes is a hallmark of only the most species-rich radiations considered here. The cichlids of Lake Malawi illustrate this pattern. Subsequent to divergence along axes of habitat and trophic morphology, lineages have experienced a diversification of male secondary sexual characteristics. Within the rock-dwelling clade, this phenomenon has been expressed in terms of male nuptial coloration [26]. Within the sand-dwelling lineage, extended male phenotypes are affected primarily. Sand-dwelling males build intricate species-specific sand 'bowers' that influence reproductive success [27]. Among marine parrotfish, a tertiary radiation of signaling phenotypes is also observed. Within the reef clade, species that share similar trophic structures differ in male mating coloration [10]. This increased variance in color usage and sexual dimorphism is correlated with differences in behavior (e.g. territoriality and a harem mating system) and is characteristic of two genera that comprise nearly 80% of all parrotfish species.

For both cichlids and parrotfish, a suite of male secondary sexual characteristics is not associated with obvious macrohabitat features (i.e. variation in color occurs within morphotypes, within habitats; Fig. 2). This is in contrast to other radiations featured here, where variance in communicatory characters, if present, is tied to divergence in macrohabitat or trophic morphology. In sticklebacks and *Anolis*, color is associated strongly with habitat [28–30]. Likewise, variation in plumage [31], bill color [32] and vocalization [33] in finches is correlated with aspects of eco-morphology.

Departures from the model

We have described a three-stage model of sequential evolution that is observed in familiar vertebrate evolutionary radiations. The evolutionary histories of the groups

we discuss are consistent with phases of the model; however, only cichlids and parrotfish have experienced all three stages in the order that we have described (Fig. 2). In other groups, the three-stage pattern is less clear. The most common departure from the model is a collapse, or absence of stages. For instance, most postglacial fish radiations do not exhibit secondary divergence in trophic morphology (Arctic char provide a counterexample [34]), nor tertiary diversification in color. In these groups, variation in habitat, morphology and communication is associated tightly; there is a single eco-morphological axis of divergence. Similarly, stage three is absent in *Anolis*. The differentiation of anoline communicatory traits has occurred, but does not represent an independent axis of diversity.

The radiation-in-stages model will not apply to all organisms; in fact, it probably does not even capture the dynamics of all cichlid radiations. For example, sexual selection on signaling phenotypes might have been the strongest force in the early stage of Lake Victoria [35] and neotropical cichlid [36] diversification. In these systems, it might turn out that the stages of radiation have been inverted (i.e. signaling evolution before habitat and trophic selection). Understanding the inherent differences in patterns of radiation will help pinpoint constraints on evolutionary diversification.

Constraints on diversification

The diversification of vertebrate lineages could be constrained by several factors, such as the environment, evolutionary history or genetic architecture. These constraints could account for some of the departures from our general framework.

Environment

The environment might be a factor constraining the radiation process. As a rule, tropical regions support greater biodiversity than do their temperate analogs [37,38], in part because there seem to be more ways for organisms to partition habitats. According to this scenario, postglacial fish radiations might be limited by the spatial homogeneity of the temperate lacustrine environment. In other words, it is possible that secondary morphological divergence does not occur in sticklebacks because benthic and limnetic settings lack suitable microhabitats for ecological selection. It is relevant that of the adaptive radiations featured here, only that of the stickleback has occurred in a temperate climate. In addition, the habitat available to sticklebacks (and other postglacial fishes) for radiation has been present only during the past 10 000 years since the last glacial maximum. The homogeneity and youth of many North American lakes might help explain why most postglacial fish radiations harbor so few species. By contrast, tropical environments provide habitats that although relatively stable, still exhibit enough disturbance to cycle organisms through phases of allopatry and sympatry [39,40].

The size of the habitat available for radiation is another feature that might limit diversification. Losos and Schluter [41] report a positive association between speciation rate and island size for Caribbean anoles, and a similar relationship between habitat area and biodiversity has been uncovered for inhabitants of coral reefs [42]. The rift

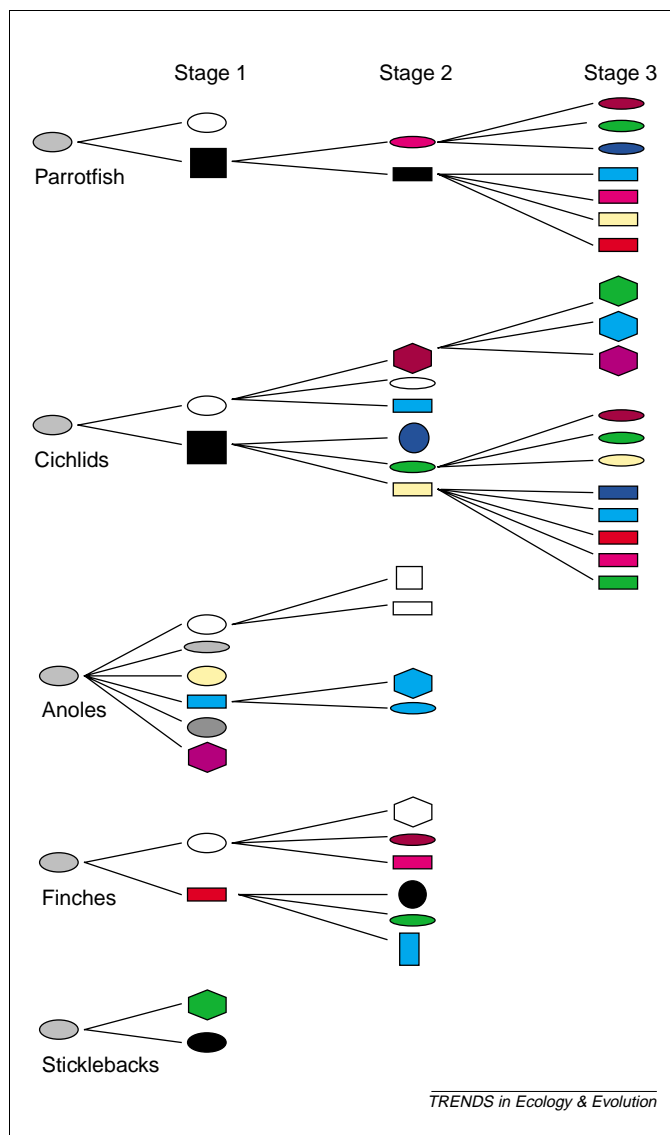


Fig. 2. Vertebrate adaptive radiations proceed to different stages of the process. Because diversity is a multiplicative feature of the number of lineages at each stage, species richness can be limited by constraints at all the axes of divergence (habitat, trophic morphology or communication). Differently shaped icons represent phenotypic variation in morphology (e.g. body size or jaw shape) and differently colored icons represent variance in signaling phenotypes (e.g. color or song) that accompany lineage splitting at each stage. Phylogenies follow [10] (parrotfish); [6,19] (cichlids); [17] (anoles); [15,16] (Darwin's finches) and [3] (sticklebacks).

lakes of East Africa are among the largest and deepest in the world, much larger than the postglacial lakes of North America. We might expect then, based on available habitat alone, to find a greater number of species of cichlids in Lake Malawi than of sticklebacks in North American lacustrine environments.

Evolutionary history

A second constraint to diversification is evolutionary history. This is exemplified best by the parrotfish oral jaw apparatus. Parrotfish represent a monophyletic, herbivorous lineage nested within the omnivorous wrasse clade [43]. As such, they have evolved strongly reinforced jaws with fused teeth, which are used to remove algae from rock, coral and seagrass habitats [21,22]. The evolution of jaw structures employed in herbivory constrains the scarid feeding repertoire. Parrotfish species lack the dramatic variation in oral jaw shape and feeding mode that is characteristic of African cichlids (or their wrasse relatives). Thus, once the initial split into seagrass and reef clades occurred, subsequent divergence along the axis of trophic morphology was limited to specialized means of herbivory.

Genetic constraints

Third, genetic constraints might bridle the extent of diversification. Genetic correlations, pleiotropy, and the quantity and type of genetic variance are all well known factors that influence the trajectory of phenotypic and population divergence. Recent modeling suggests that patterns of genetic architecture, which might maximize divergence at one stage, might effectively limit subsequent diversification.

Consider ecological selection models in which a communication trait (e.g. color) is co-opted as a mating signal to mark a fitness-determining character (e.g. size) [44,45]. Strong disruptive selection on the ecological character could drive reproductive isolation between alternative phenotypes (i.e. big-red and small-blue), leading, potentially, to speciation. In fact, this process works best if the fitness and marker traits are one and the same. This condition, thought to be unlikely [46], is met in Darwin's finches where beak morphology (i.e. a putative fitness trait) determines male courtship song (i.e. a putative marker trait [33]; see also [4] for a similar hypothesis in stickleback).

Regardless of the number of traits involved, ecological models require strong selection against intermediate or recombinant phenotypes, such that associations among traits (e.g. big-red) increase to fixation. Once fixed, marker phenotypes are unlikely to be employed in subsequent stages of the radiation process. Therefore, if the first two stages of evolutionary radiation proceed in a manner similar to ecological models, a central limitation turns out to be the number of independent loci that can serve as markers for fitness traits. Similarly, if the third phase of the radiation process occurs via the sexual selection scenario, lineages must possess a reserve of signals independent of fitness-determining characters. It is notable then, that of the radiations mentioned here, only parrotfish and cichlids [47] exhibit marked variation in communicatory traits that are not associated with ecological factors.

Uses of the model and future research

In spite of counterexamples, the pattern we describe might be a common feature in vertebrate, invertebrate and plant evolution. The primacy of disruptive ecological selection in early stages of organismal divergence is reinforced by

Box 3. Predictions of the radiation-in-stages model

If vertebrate radiations proceed as we have hypothesized, we would expect strong genetic, gametic or phenotypic associations among fitness-related traits and putative marker phenotypes for character complexes thought to be important in stage one (e.g. body size and shape). Correlations among characters might arise because of pleiotropy, epigenetic and/or epistatic interactions, in combination with strong selection [a–d]. As characters are swept to fixation during initial divergence in habitat, these phenotypes might be invisible initially to selection during subsequent stages of radiation (until sufficient genetic variation accumulates and recombination breaks associations). This is especially true in sticklebacks and finches, where mate choice depends directly on fitness-related traits [e,f].

In clades that have proceeded through stage two, we would expect to find independent sets of correlated characters associated with secondary divergence in trophic morphology (e.g. different signaling phenotypes associated with jaw and tooth shape). And, for clades proceeding through stage three, there should be a reserve of marker phenotypes inherited independently of fitness-related traits.

In recently diverged groups, quantitative trait locus (QTL) designs and other similar approaches can elucidate the patterns of inheritance for putative fitness and signaling characters. Notably, body shape is correlated with trophic morphology in a lineage of Lake Tanganyikan cichlids [g] and various fitness-related characters (pelvic and dorsal spines, dorsal spines, and gill rakers) are associated with one another [h] in the threespine stickleback.

Finally, our model makes predictions about the evolutionary forces working at each stage. We suggest that ecological selection models explain divergence in stages one and two, and sexual selection models illustrate diversification best in stage three. If this is so, there should be differences in the direction of QTL effects for factors fixed in stages one and two versus three [i]. In the first two stages of the radiation process, allelic effects should exhibit trends in directionality as a result of strong divergent selection. By contrast, allelic effects for signaling characters in stage three will not necessarily show patterns of directionality because the forces that govern signaling evolution (e.g. stabilizing natural selection and female preference) are often at odds.

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recent examples from flies [48], salmon [49] and barley [50]. Our hypothesis of radiation in stages allows us to make certain predictions about the model systems we have examined (Box 3). Given the role that communication phenotypes play in both ecological- and sexual-selection models, the most important constraint on the diversification process might be a paucity of genetic variation for means of signaling that are independent of fitness traits. The pattern of radiation in stages has been easiest to detect in groups with resolved phylogenies where character evolution has been investigated for decades. Future research with less studied organisms will clarify the generality of the pattern.

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