

KEY EVOLUTIONARY INNOVATIONS AND THEIR ECOLOGICAL MECHANISMS

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Explanations for taxonomic diversity in a particular clade often implicate evolutionary innovations, possessed by members of the clade, that are thought to have favoured diversification. We review such "key innovation" hypotheses, the ecological mechanisms involved, and potential tests of such hypotheses.

Key innovation hypotheses can be supported by evidence of ecological mechanism and by comparative tests. We argue that both are necessary for convincing support. In fact, few key innovation hypotheses are currently backed by either one.

We group ecological mechanisms of diversification in three major classes. Diversification may be spurred by innovations that: I) allow invasion of new adaptive zones; II) increase fitness, allowing one clade to replace another; or III) increase the propensity for reproductive or ecological specialization. Key innovations in different classes are likely to produce different evolutionary patterns, and therefore may be supported by different kinds of ecological evidence.

KEY WORDS: Key innovations, key adaptations, adaptive radiations, diversity, speciation rates, extinction rates.

INTRODUCTION

Accounting for the diversity of life on Earth, and for patterns of relative diversity among clades, is a central problem in ecology and evolution. Key evolutionary innovations (or adaptive breakthroughs, key adaptations, key characters or key mutations) are often invoked to account for the evolutionary success, manifested as high taxonomic diversity, of some clades. For instance, the radiation of birds is often ascribed to their acquisition of flight (Mayr, 1963), while mantle fusion has been suggested as the cause of Mesozoic bivalve diversification (Stanley, 1968). The concept of key innovation lies at the meeting point of ecology, systematics, and evolutionary biology. Differences in individual or population ecology are held to result in differences in speciation or extinction rates, and hence taxonomic diversity, among clades.

Although some authors have emphasized stochastic and historical influences on patterns of diversity (Eldredge and Cracraft, 1980; Gould, 1980, 1989; Stanley, 1979) rather than ecological factors, interest in causal explanations of diversity shows little sign of abating. There has been continued interest in evolutionary innovations in general (Larson *et al.*, 1981; McKinney, 1988; Muller, 1990; Raff *et al.*, 1990; Stebbins,

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1974) and key innovations in particular (Allmon, 1992; Farrell *et al.*, 1991; Fitzpatrick, 1988; Jensen, 1990; Liem, 1990; Mitter *et al.*, 1988; Raikow, 1986, 1988; Stanley, 1990; Wainwright, 1991). However, although key innovations are frequently invoked to account for the diversity of particular clades, the link between individual or population ecology and speciation/extinction rates has often not been made explicit. The failure to make and test this connection may be largely responsible for recent criticism of such explanations as mere adaptive storytelling (Cracraft, 1990). Linking subspecific attributes and superspecific processes, for instance by framing and testing hypotheses of key innovation, is an essential step toward a full understanding of evolution (Allmon, 1992; Maurer, 1989; Stanley, 1979; Stebbins, 1974).

The concept of "key innovation" as currently applied combines at least three distinct ecological mechanisms by which traits of individuals may influence speciation or extinction rates. These mechanisms may produce different patterns of evolution and they may require different sorts of supporting evidence. In this review we discuss definitions and tests, we outline a three-way classification of key innovations by ecological mechanism, relating examples from the literature to our classification, and we discuss expected patterns of evolution and relevant evidence for each type.

DEFINING "KEY INNOVATION"

The study of key innovations is hampered by the lack of a single, accepted definition. Miller (1949) was apparently the first to refer to "key innovations". Mayr (1963) and especially Simpson (1944, 1953) provided important early discussions of the concept. They focused on the invasion of new adaptive zones (Simpson's (1944) "quantum evolution"). A key innovation, then, was an evolutionary novelty which allows the exploitation of new resources or habitats and thus triggers an adaptive radiation.

Use of the term has evolved. While some authors remain close to the original meaning (Futuyma, 1986; Jablonski and Bottjer, 1990; Larson *et al.*, 1981; Nitecki, 1990; Wainwright, 1991), others invoke key innovations not involving the invasion of new adaptive zones, explicitly or implicitly using broader definitions (Cracraft, 1990; Eldredge, 1989; Jensen, 1990; Lauder, 1981; Liem, 1990; Van Valen, 1971; see also Rosenzweig and McCord, 1991, for an unusual definition) or discussing triggers of diversification which do not fit the original definition (Farrell *et al.*, 1991; Fitzpatrick, 1988; Raikow, 1986; Ryan, 1986; Vrba, 1984; West-Eberhard, 1983).

Clearly, evolutionary novelties which allow organisms to invade new adaptive zones are not the only kind of innovations that can be, or have been, causally connected to diversification. A full accounting of the ways in which features of individual ecology can be transduced into increased diversity will include several mechanisms. Nonetheless, it seems appropriate to emphasize the common result of these mechanisms with a single term. We favor, therefore a broad definition of "key innovation": *a key innovation is an evolutionary change in individual trait(s) that is causally linked to an increased diversification rate in the resulting clade (for which it is a synapomorphy)*. This definition is concordant with that of Erwin (1992), who held that key innovations "characterize particular clades, and are both necessary and sufficient to explain diversification within the clade". Under the original, narrower definition, many of the "key innovations" found in the literature (in particular, those listed here in Tables 2 and 3) would be excluded.

An increased rate of diversification may reflect increased speciation, decreased extinction, or both. The relative importance of these two rates in controlling diversity has been debated (e.g. Gilinsky, 1981), and their contributions surely vary from case

to case. Furthermore, increased speciation rates may result from several different sorts of processes: those favouring the formation, the survival, or the differentiation of isolated populations (Allmon, 1992).

We intentionally do not restrict the kinds of trait changes which may be considered as key innovations. Some authors have held that innovations must be qualitatively new structures or properties, not just gradual or quantitative changes (Cracraft, 1990; Mayr, 1960; Muller, 1990). On the other hand, Jablonski and Bottjer (1990) explicitly allowed "small" changes in function as innovations, while Kochmer and Wagner (1988) discussed size (clearly a quantitative character) in the context of explaining passerine bird diversity. When considering possible causes of diversification, it does not seem logically necessary to exclude quantitative differences. In some cases, furthermore, an "innovation" may not represent a single evolutionary transition, but rather a character complex or a number of functionally related traits: for instance, those which together were necessary for insect phytophagy (Mitter *et al.*, 1988), or those involved in the novel jaw morphology and function of cichlid fishes (Liem, 1974).

TESTING KEY INNOVATION HYPOTHESES

A key innovation hypothesis generally takes the form "clade X is diverse (compared to its sister clade) because its ancestor and member species possess(ed) trait Y". For instance, one could hypothesize that infaunal bivalves are diverse because they acquired mantle fusion (Stanley, 1968). However, such ideas are much easier to propose than they are to test (Cracraft, 1990; Erwin, 1992). Convincing support for a hypothesis of key innovation will include two components: first, an ecological, or "functional" argument, and second, a comparative test.

The ecological/functional argument will consist of a hypothesis or set of hypotheses linking the putative key innovation to increased speciation or decreased extinction rates (compared to the sister group). For instance, it might postulate that possession of the key innovation deters predators or parasites, allowing higher population density, which in turn confers resistance to extinction (see Farrell *et al.*, 1991, for plant latex canals; Stanley, 1990, for mantle fusion in bivalves). Allmon (1992) has provided a thorough compendium of possible ecological factors that would increase speciation rates.

Each hypothesis in the ecological argument may be supported or tested independently, for instance by comparing extant species lacking and possessing the trait in question. However, careful tests of this type appear to be extremely rare. The relevant sort of ecological argument differs greatly among key innovation hypotheses, and in fact provides the basis of the classification outlined below. The ecological argument is important three reasons. First, building and testing an ecological argument affords opportunities to falsify a key innovation hypothesis. Second, a key innovation hypothesis without some ecological basis is arbitrary without a mechanism. Third, a well-supported ecological argument can give a key innovation scenario plausibility.

However, even a detailed argument, based on a unique key innovation and its supposed consequences, represents only a single observation of the trait-diversity association. Thus, it is often argued that the observed difference in diversity is only stochastic or that it is due to some confounding influence (Jensen, 1990; Landers, 1981, 1982; Mitter *et al.*, 1988). This issue can often be resolved with the use of a comparative test (Fitzpatrick, 1988; Jensen, 1990; Mitter *et al.*, 1988; Farrell *et al.*, 1991; Weigmann *et al.*, in press). A number of clades which independently acquired the same or similar innovations (preferably in more or less comparable ecological circumstances) are compared with their sister clades which lack the innovation in question. The

correlation of diversity with possession of the presumed key innovation is then tested statistically, generally with a sign test. The sign test is unfortunately sensitive only to the direction, not the magnitude, of diversity differences: a pattern where sister clades include 4 and 5 species is treated no differently from one in which sister clades include 4 and 500 species. Without much more understanding of expected diversity patterns among evolving lineages (Guyer and Slowinski, 1991, 1993; Heard, 1992; Savage, 1983) we cannot predict the null distribution of diversity differences among sister clades, so we have no option but to use a non-parametric test despite its lack of statistical power.

"Supporting" a key innovation argument by reference to another diverse group with a similar innovation does not constitute a rigorous comparative test (Cracraft, 1990). Rather, the putative key innovation must be clearly (if perhaps broadly) defined *a priori*, and all instances of the innovation within a large group of interest must be tabulated. Alternatively, if a key innovation is suggested not *a priori* but by its occurrence in one diverse clade, a comparative test can be conducted using similar innovations in other clades (perhaps excluding clade that inspired the hypothesis in the first place). Very few such tests have been carried out (Table 1, 2, 3), perhaps because of the difficulty of defining "similar" innovations rigorously.

We emphasize that, alone, neither a comparative test nor an ecological argument will be fully convincing. The two are distinct but complementary and mutually reinforcing elements of a key innovation explanation. The comparative test establishes a correlation between the supposed key innovation and diversity. This suggests but does not demonstrate a causal relationship. The ecological argument establishes and may test the mechanism by which that causation is thought to act.

These tests allow us to avoid a vexing problem in establishing key innovation hypotheses: the problem of multiple synapomorphies (Erwin, 1992, his Figure 1). A diverse clade may be characterized by many innovations (synapomorphies), any one of which might account for the diversity. Since the bounds of the clade whose diversity needs explaining may also be in doubt, higher or lower taxonomic level synapomorphies might also need to be considered (Coddington, 1988; Cracraft, 1990). In such cases, it may not be clear which innovation is implicated in driving diversification. For instance, Stanley (1990) separately invoked wall plate structure and internal fertilization to explain the success of balanoid barnacles. The proponent of a key innovation hypothesis must demonstrate that one of the multiple synapomorphies is responsible for the diversification. This is not difficult in principle if both comparative tests and ecological arguments are brought to bear. Ecological arguments may establish that only one of the synapomorphies defining the clade in question can be causally linked to increased speciation or decreased extinction rates. Comparative tests can be used to examine the association of each synapomorphy with diversity over a set of clades possessing similar innovations.

Key innovation hypotheses have been criticized on the grounds that every clade has at least one synapomorphy, so a creative story-teller should be able to propose a key innovation hypothesis for every clade. We stress that this is only a problem if the hypotheses are never tested. Under the scrutiny of comparative and ecological tests, some will stand up, and others will be discredited.

THREE ECOLOGICAL ROUTES TO DIVERSIFICATION

Explanations of diversification based on key innovations must be sought in connections between particular traits of individuals and rates of speciation and extinction. As we imply above, it will impossible to present a fully convincing

explanation without directly considering how innovations and diversification are linked by the ecology of individuals and populations. There are at least three major classes of mechanisms for this linkage. We recognize that, as in most classifications of biological processes, there are some grey areas. However, the assignment of a particular key innovation hypothesis to one of these classes is a first step toward identifying the kinds of information required to support an ecological argument.

I. "New Adaptive Zone" Key Innovations

The most frequently discussed type of key innovation is that in which the appearance of a novel structure allows a species to invade a new and relatively empty adaptive zone, leading to an adaptive radiation in the absence of competing taxa (Miller, 1949; Simpson, 1944, 1953). An "adaptive zone" is a general way of life (Simpson, 1953) or a set of related niches (Stanley, 1979). The concept is somewhat vague, but nonetheless useful. Some putative "new adaptive zone" key innovations, taken from the literature, are listed in Table 1. This table and Tables 2 and 3 list key innovations which have been hypothesized. They are not all necessarily well documented or correct. In fact, the most striking impression given by this tabulation of key innovation hypotheses is how little effort has been devoted to testing them!

The essential element in explanations of the "new adaptive zone" type is that as a result of a newly acquired trait, new habitat or resources become available. The species or lineage therefore becomes free to diversify without (or with reduced) competition from other lineages. Not every innovation which results in a change of adaptive zone would be expected to lead to diversification. The "new" (to the invading species) zone might or might not be free of competition (Hardy, 1985), or the new way of life might be limited in terms of resource availability or opportunity for further speciation. Mayr (1960) gave several examples of adaptive shifts not followed by diversification, including the evolution of herbivory by giant pandas. Furthermore, the ancestral lineage may continue to diversify in the old adaptive zone (Miller, 1949). Although reduced competition has generally been invoked, escape from predators or parasites might also be involved when invasion of the new adaptive zone also involves a move to a new habitat or the adoption of new activity patterns.

Either speciation or extinction rates might be involved in diversification in a new adaptive zone. Both have been assumed to respond, in macroevolutionary models, to the proportion of "available" (competitor-free) niches (Erwin *et al.*, 1987; Maurer, 1989; Rosenzweig, 1975; Sepkoski, 1979, 1984; Walker and Valentine, 1984). Extinction rates might be expected to decrease with reduced competition, either because the threat of competitive exclusion is removed (Bengtsson, 1989; Gause, 1934; Ricklefs, 1990, p. 438ff; Stanley, 1987, p. 85), or because species with larger ranges (competitive release, Diamond, 1975; Karron, 1987) or higher population densities (Pimm *et al.*, 1988; Schoener, 1991) are more resistant to stochastic extinction. Speciation rates, on the other hand, are likely to increase as larger ranges and population sizes result in increased production and survival of peripheral isolates (Allmon, 1992; Farrell *et al.*, 1991; Rosenzweig, 1975; Vermeij, 1977), or "diversifying selection" could lead to the exploitation of various unutilized resources. (Mitter *et al.*, 1988; Rosenzweig and Taylor, 1980).

Mitter *et al.* (1988) considered insect phytophagy as a key innovation in one of the few well documented examples (Table 1). They examined independent origins of phytophagy and found the resulting phytophagous clades to be consistently (11 of 13 times) more diverse than their sister clades. They also discussed (but did not test) several possible "new zone" ecological arguments for the cause of this difference.

Table 1 Some possible type I ("new adaptive zone") key innovations. These examples are postulated in the literature, but inclusion here does not imply that a particular hypothesis is well supported or necessarily correct.

Group(s)	key innovation	new zone	ecological argument	comparative test	reference	comments
mammals	homeothermy	nocturnality; cold climates	avoid competition from dominant reptiles	X ^a birds	Liem, 1990	but see Van Valen, 1971; Benton, 1979
snakes	jaw structure: decoupled mandible halves, etc.	large prey	none	none	Liem, 1990 Gaus, 1961	
bats	flight	nocturnal flight	various, including flying insects as food	X birds	Hill and Smith, 1984	
various Unbelliferae	furunculocannins	dry habitats	UV screening; ↑ root growth	T ^a 62 genera	Berounbaum, 1983 Mathias, 1965	see also in Table 2
<i>Aneides</i> (Plethodontidae)	rearranged capels; premaxillary fusion	arboreality (locomotion and feeding)	avoid competition from <i>Plethodon</i>	none	Larson <i>et al.</i> , 1981	new zone not entirely empty
various phytophagous Insecta	various	phytophagy	↑ resource base; lack of competition among phytophages (Strong <i>et al.</i> , 1984)	C ^a 11/13	Milner <i>et al.</i> , 1988	
Bivalvia	mantle fusion and siphon	infauna	lack of competition and variety of niches	none (but habit polyphyletic)	Stanley, 1968, 1974, 1977	some non-siphonate infaunal molluscs were present
rudist bivalves	ligament invagination (allows uncoiled growth)	"elevator" and "recumbent" forms on soft substrata	lack of competition	none	Skelton, 1985	but see balanoid barnacles in Table 2
Pholadacea (wood-boring bivalves)	7 "innovations" allowing wood boring; none singled out	aquatic wood boring niche	otherwise empty niche	none	Hoagland and Turner, 1981	

Table 1 Cont'd.

Group(s)	key innovation	new zone	ecological argument	comparative test	reference	comments
<i>Citharus</i> (Citharus)	combed mandibles	high intertidal	avoid competition from balanoid barnacles	none	Stanley and Newman, 1980	compared to other Citharinoidea
labrid fish	strong pharyngeal jaw	urchin and mollusc crushing	otherwise empty niche on coral reefs	none	Wainwright, 1991	note overlap with labroid KI in Table 3.
passeriforms	foot design	perching	none	none	Raikow, 1982	but see Raikow, 1986
ants	burrowing? (unclear)	"social, terrestrial predators"	lack of competition	none	Hölldobler and Wilson, 1990	
anoline lizards	subdigital pads	arboreality	lack of competition, variety of arboreal niches	none	Peterson, 1983	
insects (except Collembola, Protura, Diplura)	ovipositor and resistant egg	oviposition in non-cryptozoic habitats	variety of niches, otherwise empty	X spiders and mites	Zeh and Zeh, 1989	within Insecta, oviposition habitat diversity is correlated with taxonomic diversity. For spiders, see also Table 3
irregular echinoids	various trails allowing burrowing	soft sediments	lack of competition	none	Smith, 1984	
Elephantidae	shearing molars; other associated chewing traits	not clearly defined	none	none	Maglio, 1973	modern low diversity attributed to human predation

* comparative "test": anecdotal, citing other examples (X); taxonomic, comparing taxonomic groups in species/family ratios, etc. (T); or cladistic, comparing diversities of sister clades (C)

These include the large resource base of plant tissues, the rarity of competition among phytophagous insects, and the diversity of niches available to phytophages, all of which may contribute to reduce extinction rates and to increase the establishment and survival of peripheral isolates.

Because "new zone" key innovations are associated with empty, or at least underexploited, adaptive zones, they might be expected to show a broad-scale temporal pattern. Such key innovations should have been most common early in the history of life, and perhaps following mass extinctions (Hansen, 1987; Rosenzweig and McCord, 1991; but see Erwin *et al.*, 1987). Unfortunately, well-understood examples of type I key innovations are too few (if indeed any qualify as "well-understood") to evaluate this prediction. In contrast, this pattern is not to be expected in either of the other two types of key innovation we discuss (pattern differences among types of key innovation are summarized in Table 4).

Myers (1960), Stanley (1975), and others have discussed the analogous situation where radiation occurs after colonization of a new geographical area, such as a new lake or island, rather than a new adaptive zone. Erwin (1992) treats these as "economic", as opposed to adaptive, radiations. While such radiations do not depend on evolutionary novelty, so there is no key innovation, they do depend on ecological opportunity and would be expected to produce similar patterns.

Arguments of the "new zone" type are largely dependent on strong effects of interspecific competition on community structure, although escape from predators or parasites might also be invoked. The extent and importance of such effects have been disputed (Connell, 1983; Goldberg and Barton, 1992; Gurevitch *et al.*, 1992; Roughgarden, 1983; Schoener, 1983; Strong *et al.*, 1984a; papers in Strong *et al.*, 1984b), and at some times or for some groups competitors may not be important. Furthermore, Stanley (1974) has advanced an opposite argument, that diversification may be slower under reduced competition. Merely demonstrating reduced numbers of competitors in a new adaptive zone is not, then, sufficient to justify a hypothesis of key innovation; the ecological and comparative arguments are essential.

II. "Increased Fitness" Key Innovations

Not all evolutionary innovations produce the sorts of adaptive shifts discussed above; more likely, only a small fraction do so. However, evolutionary changes which increase individual fitness, such as increases in feeding efficiency or pathogen resistance, should be common whenever selection operates. Can an innovation which simply confers increased fitness produce diversification in the lineage possessing it, at the expense of other lineages? Such arguments appear in the literature (Table 2).

We include here at least two cases originally proposed as potential "new adaptive zone" key innovations. Berenbaum (1983) and Farrell *et al.* (1991), following Ehrlich and Raven (1964; see also Van Valen, 1971) considered innovations in plant chemistry that reduce herbivory as invasions of new adaptive zones. However, if chemical defenses affect geographical range and niche breadth only indirectly via reduced herbivory, it seems more appropriate to see this as increased plant fitness rather than entry into a new way of life. This corresponds to the use of the term "adaptive zone" in a slightly narrower sense, one perhaps closer to the original meaning (Simpson, 1953; see also Wainwright, 1991).

The ecological arguments supporting "increased fitness" key innovations are similar to those for "new zone" key innovations, but the avoidance of competitors is not involved. Instead, increased competitive ability attained through such changes as increased efficiency of water use (Knoll, 1984), decreased predation or parasitism (Berenbaum,

Table 2 Some possible type II ("increased fitness") key innovations. These examples are postulated in the literature, but inclusion here does not imply that a particular hypothesis is well supported or necessarily correct.

Group(s)	key innovation	ecological argument	comparative test	reference	comments
most teleosts	closed swim bladders; gas secretion	allows vertical migrations to follow prey	X* eels	Liem, 1990	see also in table 3 (acanthopterygians)
artiodactyls	astragalus	more efficient running; outcompete perissodactyls and escape predation	none	Simpson, 1953	but see Janis, 1976, Cifelli, 1981
artiodactyls	rumination	more efficient digestion; outcompete perissodactyls	none	Colbert, 1969 Young, 1962	but see Janis, 1976, Cifelli, 1981
various angiosperms	latex/resin canals	↓ herbivory; ↑ range and population density; ↑ speciation, ↓ extinction	C* 13/16	Farrell <i>et al.</i> , 1991	argued as a case of "new adaptive zone"
various Umbelliferae	furano-coumarins	↓ herbivory; ↑ range; ↑ speciation	T* 62 genera	Berenbaum, 1983	see also in Table 1
archosaurs	limb posture; locomotor ability	outcompete Therapsida	none	Bunaparte, 1982 Chang, 1980	but see Benton, 1979, 1987
archosaurs	endothermy	outcompete Therapsida	none	Bakker, 1971, 1972, 1975	but see Benton, 1979, 1987
rodents	persistent incisor growth	outcompete multituberculates	none	Wilson, 1951	
balanoid barnacles	tubiferous wall	rapid growth; outcompete chthamoids	X scleractinian corals, rudist bivalves	Stanley and Newman, 1980	but see rudists in Table 1 and balanoids in Table 3

Table 2 Cont'd.

Group(s)	key innovation	ecological argument	comparative test	reference	comments
comatulid crinoids	loss of stalk (mobility)	resistant to teleost fish predation; replace stalked crinoids	none	Meyer and Macurda, 1977	
early Devonian trimerophytes	vascular advances: tracheids with scalariform pits	better water conduction; outcompete rhyniophytes by overtopping	X next entry	Knoll, 1984	
middle Devonian progymnosperms	secondary xylem; bordered-pit tracheids	better water conduction; outcompete trimerophytes	X previous entry	Knoll, 1984	
early Carboniferous pteridosperms	seed	better establishment and early growth of sporophyte; outcompete progymnosperms	none	Knoll, 1984	

* comparative "test": anecdotal, citing other examples (X); taxonomic, comparing taxonomic groups in species/family ratios, etc. (T); or cladistic, comparing diversity of sister clades (C).

1983; Farrell *et al.*, 1991), or faster growth rates (Stanley and Newman, 1980) is usually invoked. This results in an expanded geographic or ecological range, or increased population density, which in turn is translated into increased speciation and/or decreased extinction rates through success of peripheral isolates as was the case for "new zone" key innovations.

One of the best documented cases of an "increased fitness" key innovation is that of latex and resin canals in plants (Farrell *et al.*, 1991). Of 16 clades which evolved these structures independently, and for which sister groups are known, 13 are more diverse than their sister clades. This is strong evidence that possession of canals does spur diversification. The ecological argument involves increased fitness via herbivore resistance. The hypothesis that possession of canals reduces herbivory and protects against pathogens is well supported for many taxa. Farrell *et al.* (1991) also found that canals have population-level consequences: Peruvian species with canals have greater niche breadth and local abundance than sympatric relatives lacking canals. Greater abundance impedes extinction (Pimm *et al.*, 1988; Schoener, 1991). With both a comparative test and a relatively well-supported ecological mechanism, the resin canal example is probably the most convincing argument to have been made for the role of a key innovation.

The range expansion or increased population density arising from a type II key innovation is usually supposed to come at the expense of one or more other taxa, through competitive displacement. Therefore, "increased fitness" key innovations, unlike the two other types we discuss, may be associated with a paleontological pattern of competitive replacement. Such patterns, however, are difficult to document and have recently been in disfavor (e.g. Benton, 1987; Cifelli, 1981; Gould and Calloway, 1980; Marshall *et al.*, 1982; Rosenzweig and McCord, 1991; Valentine *et al.*, 1991). It has been suggested that competitive displacement is more common among plants than among other organisms (Knoll, 1984). Mechanisms which do not directly involve competition, such as increased resistance to abiotically induced extinction, have received less attention (but see Benton, 1987).

III. "Specialization" key Innovations.

The third route for the production of diversity involves innovations which increase potential for reproductive or ecological specialization. The result of such an innovation is likely to be an increased speciation rate and an increase in the number of species which coexist within a clade. While reproductive and ecological specialization may involve different characters and different ecological processes, we treat them together to emphasize major similarities. Most important is that because specialization allows subdivision of a niche or range, the increase in species number resulting from type III key innovations need not involve either an adaptive shift (type I key innovation) or the competitive displacement of any other species (type II key innovation). Indeed, as Stanley (1990) implies, in type III scenarios the innovation in question need not necessarily be adaptive at the individual level. Examples of type III key innovations proposed in the literature are listed in Table 3.

A) Reproductive specialization

Reproductive "specialization" key innovations result directly in an increase in the rate of formation of small, isolated populations. Evolutionary changes in dispersal capabilities which have consequences for diversity are an example. The correlation between non-planktotrophic larvae and species diversity has been well studied in both

Table 3 Some possible type III ("specialization") key innovations. These examples are postulated in the literature, but inclusion here does not imply that a particular hypothesis is well supported or necessarily correct.

Group(s)	key innovation	mechanism	ecological argument	comparative test	reference	comments
echinostome bryozoans	larval brooding	R ^a	↓ dispersal distance; ↑ isolation, speciation	X ^a molluscs	Taylor, 1988	argues example of effect hypothesis
various Mollusca	lecithotrophic larvae	R	↓ gene flow; ↑ speciation but also ↓ range; ↑ extinction	T ^b (various)	Hansen, 1980 Jablonski, 1980 Shuto, 1974	
angiosperms	carpel closure	R	dispersal mechanism became independent of seed morphology; new dispersal modes possible; ↑ isolation	none	Doyle and Donoghue, 1986	
oscines, Furnarii, Tyranni (passeriforms)	complex syntax	R	complex male recognition; ↑ speciation	T 3/3	Ralkow, 1986 Fitzpatrick, 1988 Vernelji, 1988	
Hawaiian <i>Drosophila</i>	lekking	R	stronger sexual selection; combined with founder effects results in rapid divergence	none	Ringo, 1977 Templeton, 1979	
Anura	specialized amphibian papilla	R	↑ variation in possible mating calls; ↑ speciation	T 13 families	Ryan, 1986	
placental mammals	lactation, producing social bonds	R	↓ effective population sizes; ↑ inbreeding; rapid fixation of gene rearrangements; ↑ speciation	none	Wilson <i>et al.</i> , 1975	
fiddler crabs subgenus <i>Celura</i>	more complex social behavior	R	complex male recognition system; ↑ speciation	none	West-Eberhard, 1983	

Table 3 Cont'd.

Group(s)	key innovation	mechanism	ecological argument	comparative test	reference	comments
parrots	"clatunishness"	R	↑ behavioral isolation	none	Hardy, 1966	
spiders	ballooning	R	better dispersal; ↑ frequency of founder events	none	Zeh and Zeh (1989)	see also insects in Table 1 - egg protection also invoked
various insect parasites	parasitism	R	highly fractionated gene pools; ↑ speciation rate	T comparing size of 20 parasitic and 10 non-parasitic families	Price (1977)	but see Wiegman <i>et al.</i> 1993; sister-clade test rejects hypothesis
halanoid barnacles	internal fertilization	R	↑ reproductive isolation; ↑ speciation	none	Stanley (1990)	but see Table 2
acanthopterygian fishes	protrusile premaxilla (jaw structure)	E ^a	allow specialization of feeding mechanism	none	Schaeffer and Rosen, 1961	see also Table 2
labroid fishes	pharyngeal jaw structure	E	free oral jaw from food processing; can specialize for collection	X Belontiiformes	Jensen, 1990 Liem, 1974 Stanssy and Jensen, 1987	not clear if comparative test is a priori
passerines	small size	E	"more ways of life" available to small organisms	X rodents, bats	Kochmer and Wagner, 1988	
Alcelaphine bovids	specialized feeding niche; independence of water	E	↑ directional selection in bad years, compared to generalist sister clade	C ^b 5 million years of species turnover; X elands vs. kudus	Vrba, 1984	argued an example of effect hypothesis
gekkonid lizards	foot pads (spinose Oberhautchen layer)	E	↑ flexibility in locomotion	X <i>Anolis</i>	Russell, 1979	ecological mechanism not well developed

^a "flexibility": ecological (niche) specialization (E); or reproductive (mating system) specialization (R).

^b comparative "test": anecdotal, citing other examples (X); taxonomic, comparing taxonomic groups in species/family ratios, etc. (T); or cladistic, comparing diversity of sister clades (C).

molluscs (Cohen and Johnston, 1987; Hansen, 1980, 1983; Jablonski, 1980, 1982, 1986; Scheltema, 1971, 1977, 1978; Shuto, 1974) and cheilostome bryozoans (Taylor, 1988). Planktotrophic larvae in both groups have greater dispersal abilities than do non-planktotrophic forms. Species with planktotrophic larvae should therefore have larger geographic ranges and higher rates of gene flow compared to non-planktotrophic forms (Gooch, 1975; Janson, 1987). Differences in gene flow can have direct effects on speciation rates: non-planktotrophic forms, with their tendency to form genetically isolated populations, speciate more often. A similar correlation between reduced vagility and diversity has been identified in other taxa (Templeton, 1979, *Drosophila*; Echelle and Kornfield, 1984, fish; Vrba, 1987, mammals; see also Rosenzweig, 1975).

An important caveat comes from Bleiweiss' (1990) work on hummingbirds. Bleiweiss compared vagility and ecological specialization between the Phaethornithinae (approx. 35 species) and the Trochilinae (approx. 295 species). In this case, the diverse trochilines are both more vagile and less ecologically specialized than the depauperate phaethornithinines. Similar examples of a positive correlation between increased vagility and diversity have been found in molluscs (Vermeij, 1987) and ungulates (Vrba, 1980; however, vagility in this example is confounded with ecological specialization), and argued for spiders (Zeh and Zeh, 1989). These counter examples illustrate an important point: hypotheses involving the effect of vagility on diversification depend on the geographic context in which the radiation takes place. Although vagile species may experience increased gene flow between populations, they may also be superior colonizers of new regions (MacArthur and Wilson, 1967; Williamson, 1981; Zeh and Zeh, 1989). Intermediate levels of vagility may actually promote speciation (Allmon, 1992; Taylor, 1988). Bleiweiss (1990) argues that that this is most likely to be the case when there is extreme environmental heterogeneity or topographic complexity. In a similar vein, Slatkin (1987) has discussed situations where gene flow between populations might promote the production of reproductively isolated populations.

In reviews of parasite biology Price (1977, 1980) discussed changes in population structure that are likely to follow the adoption of a parasitic habit. Two important features of parasite population structure are a high frequency of founder events as single females duplication give rise to populations in new hosts, and highly fractionated gene pools as parasite populations in different host individuals are isolated from one another. Combined with high reproductive rates, these can lead to rapid differentiation of populations, so Price (1977, 1980) suggested that parasitism should be linked to diversification. However, this prediction has not been well tested. It appears not to hold for carnivorous parasitic insects: parasitic insect clades are if anything *less* diverse than their non-parasitic sister clades (Wiegmann *et al.*, 1993).

Changes in mating systems (reproductive morphology or behavior) which increase the likelihood of reproductive isolation have also been associated with increased speciation rates. For instance, female preference for mating calls is an important behavioral isolating mechanism in frogs, no two species having the same call (Blair, 1964; Capranica, 1976). Ryan (1986) found a strong correlation among families of anurans between species diversity and the complexity of the amphibian papilla of the inner ear. More complex papillae allow detection of a greater range of frequencies (Lewis, 1981) and presumably allow a greater diversity of recognizable calls. A similar argument has been advanced for diversity and the passerine syrinx (Fitzpatrick, 1988; Raikow, 1986; Vermeij, 1988). The causality has also been argued in reverse; species in more diverse clades may be under more pressure to evolve effective species-recognition mechanisms (Williams and Rand, 1977). Here a good phylogenetic reconstruction, including the relevant character state transitions, is indispensable. If

flexibility in mating calls is conferred by an innovation that arose once in the clade's common ancestor, mating call diversity can be a cause of taxonomic diversity but not a result of it.

West-Eberhard (1983) has discussed the connection between sexual selection and high speciation rates in detail. In general, innovations which result in a greater potential for sexual selection increase the probability of morphological diversification and speciation. Templeton (1979; see also Carson, 1978) invoked a combination of strong sexual selection due to lekking behavior and repeated founder effects to account for the diversity of Hawaiian *Drosophila*. Furthermore, other innovations in mating systems may be especially efficient at producing diversity when they are exposed to sexual selection, which can produce very rapid evolutionary change (O'Donald, 1977) and reproductive isolation (Ringo, 1977).

A propensity among certain plant lineages to form Polyploids and especially amphiploids (Jackson, 1976; Lewis, 1980) might also be thought of as a type III key innovation. Because polyploidy results in immediate reproductive isolation, lineages where it is common should have high speciation rates (Stebbins, 1982). Levin and Wilson (1976) found a positive correlation between high chromosome numbers (which reflect, in part, the occurrence of polyploidy) and species diversity in seed plants.

B) Ecological specialization

Increased ecological specialization may also produce diversification, although less directly than is the case for reproductive specialization. Here, reproductive isolation must evolve secondarily, possibly as a consequence of different habitats or selection against intermediate forms.

An important set of key innovations make further morphological, physiological, or behavioral specialization possible ("morphopotentiality"). For instance, new structural features in the pharyngeal jaw of labroid fishes are said to have freed the oral jaws from the task of food preparation, allowing them to specialize for food collection (Fryer and Iles, 1969; Jensen, 1990; Liem, 1974; Liem and Osse, 1975; Stiassney and Jensen, 1987). As a result the clade has been able to "specialize progressively into diversified subzones, ramifying prodigiously" (Liem, 1974, p. 425). Cichlids, the largest family of labroids, have adapted the oral jaw for such diverse roles as mollusc crushing, fish capture, and phytoplankton grazing. Note that increased morphopotentiality in reproductive structures (genitalia) would be expected to produce diversity by a "reproductive specialization" route.

The connection between ecological specialization (stenotopy) and diversification has been discussed by several authors (Eldredge, 1979; Eldredge and Cracraft, 1980; Novacek, 1984; Stanley, 1985; Vrba, 1980, 1983, 1984). The usual argument holds that ecological generalists are less sensitive to environmental variation and therefore less prone to isolation and divergent selection among populations than specialists. An evolutionary change favoring specialization that persists in descendent taxa can cause increased diversity in the resultant clade. This is an "effect" in the sense of Vrba (1980, 1983). For instance, Vrba (1984:76) argues that directional selection "acts on populations whose resource base has been removed or severely altered by environmental change". Narrowly specialized species are most likely to be affected, while generalists with alternative habitats are more likely to be under stabilizing selection. Vrba (1984) accounted in this way for the high diversity of alcelaphines (wildebeest and relatives), which require open grassland, compared to their sister taxon, the impala, which is more flexible and feeds in bush, grassland, and ecotones.

Benton (1990) connected increased ecological specialization and diversity on a much broader scale. He invoked increasing specialization over geologic time to account for increasing world-wide taxonomic diversity over the Phanerozoic. This hypothesis was supported by a pattern in increased alpha (single site) diversity in well-preserved terrestrial tetrapod assemblages from the Carboniferous through the Tertiary. However, Benton (1990) did not attempt to explain diversity in particular clades.

Because both reproductive and ecological "specialization" key innovations involve niche subdivision rather than niche expansion, species in a more diverse clade might often be expected to have smaller geographic ranges or population densities. Vrba (1984) reported that most alcelaphines have low population densities compared to impalas, their low-diversity sister taxon. As a result, "specialization" key innovations are not likely to be linked to low extinction rates. In fact, small ranges and low population densities may result in relatively high extinction rates (Hansen, 1980; Stanley, 1990; Taylor, 1988), so high net diversification must be driven by high speciation rates. This stands in sharp contrast to the situation for type I and II key innovations, where species in the more diverse clade might have equal or greater ranges or densities, and therefore also lower extinction rates.

Type III and multistep key innovations

Some key innovations may be difficult to identify or classify because evolutionary changes triggered by a type III key innovation are themselves key innovations of another type. After a type III key innovation, a clade will produce many more specialized variants, which may only subdivide the niche occupied by the ancestral species. However, some variants may also expand beyond the ancestral niche. A possible consequence of the proliferation of forms, particularly when the specialization is ecological, is the production of new species that are capable of exploiting new resources or habitats, or which represent "improvements" that can displace competing taxa. In other words, the initial propensity

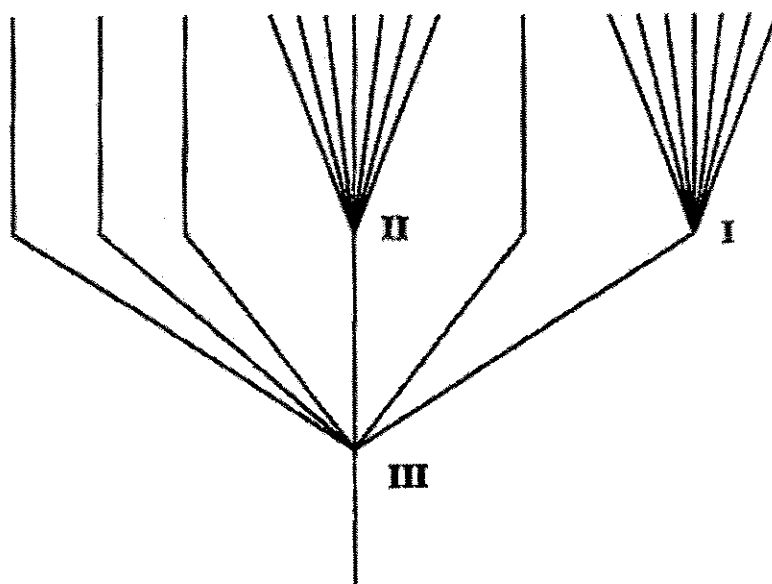


Figure 1 A hypothetical phylogeny illustrating the tendency for type III key innovations to trigger further, secondary radiations. The type III key innovation conferred on the lineage a propensity to form isolates and/or variants, resulting in the first radiation. Some of these variants themselves possessed innovations that allowed them either to invade a new adaptive zone (type I key innovation) or to displace other taxa competitively (type II key innovation); in each case a secondary radiation resulted.

for specialization arose as a type III key innovation, but some of the particular changes producing specialists may in turn constitute type I or type II key innovations and produce secondary radiations (Figure 1). When this occurs it dramatically accelerates diversification of the clade as a whole.

For instance, returning to the case of labroid fishes, the trigger for diversification has been argued to be morphopotentiality in oral jaw design (Jensen, 1990). This presumably allowed a generalist-feeding ancestor to radiate, producing many specialized descendants: a type III key innovation in our scheme. However, some of these descendants possessed features that allowed them to exploit resources not available to the generalized ancestor (Liem, 1974). Features which correspond to type I key innovations may have led to secondary radiations. Alternatively, some descendants may have acquired fitness advantages over their potential competitors (type II key innovations; Liem and Osse, 1975). A clearer picture of the relative roles of specialization and the invasion of new adaptive zones in labroid diversification will require (at least) more detailed knowledge of labroid phylogeny and paleoecology.

In an argument that may be related, Vermeij (1973) held that there is a general trend among plants and animals toward greater versatility of form, and that this has resulted in increased mechanical efficiency and effectiveness in exploiting resources. This would imply a role for versatility in producing advances in fitness, some of which might be type II key innovations.

Table 4 Summary of major differences in patterns of evolution expected to result from types I, II, and III key innovations.

Pattern	type I	type II	type III
more common early in earth history (or after mass extinctions)	Yes	No	No
associated with competitive replacement of other taxa	No	Yes	No
change in average geographic range or population density in species possessing the key innovation	likely ↑	↑	likely ↓

CONCLUSION

A full understanding of evolution, diversity, and the history of life will require careful study of the ways in which traits of individuals influence speciation and extinction rates. When evolutionary change in an individual trait or traits is responsible for increased diversification, we recognize the new trait(s) as a key innovation.

Convincing support for a hypothesis of key innovation will include both a comparative test and an well-supported argument for an ecological mechanism. Very few studies have mustered both, and a large number of key innovation hypotheses lack any such support (Tables 1-3). The ecological mechanisms for key innovations suggested so far fall into three major classes: invasion of new adaptive zones, increases in fitness generally leading to competitive replacement, and increased propensity for specialization, either reproductive or ecological.

Key innovations with different ecological mechanisms are likely to show different evolutionary patterns (summarized in Table 4) and they will be supported by different kinds of evidence. Assigning a key innovation hypothesis to one of the three classes provides guidance for the design of tests and development of a supporting ecological argument. For instance, a type I or II hypothesis would be supported by data suggesting greater average population density in species possessing the key innovation, while a type

III hypothesis would be undermined by the same data. Grouping putative key innovations as we do here improves our ability to construct and test clear, unambiguous, and useful key innovation hypotheses, and therefore ultimately to understand the evolutionary processes that lie behind patterns of taxonomic diversity.

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