Contingent Predictability in Evolution: Key Traits and Diversification

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Abstract.—Key innovations have often been invoked to explain the exceptional diversification of particular groups. However, there are few convincing examples of traits that are repeatedly and consistently associated with increased diversification. The paucity of such cases may reflect the contingent nature of the diversifying effect of key traits. These contingencies can be viewed as statistical interactions between the trait and at least three kinds of factors: (1) other taxa, (2) other traits of the group itself, and (3) the physical environment. I describe tentative examples in each of these categories: (1) a dampening of the diversification of clades with image-forming eyes by groups that earlier evolved such eyes, (2) an effect of growth form (woody or herbaceous) on the diversifying effect of biotic seed dispersal in angiosperms, and (3) an effect of atmospheric CO_2 level on the diversifying effect of C_4 photosynthesis in monocots. These examples suggest the need for more complex analyses of the relationship between possible key traits and diversification. They also suggest that radiations may be predictable given certain circumstances, thus supporting a view of evolution as both predictable and contingent. Ironically, a certain degree of predictability may be critical to arguments for evolutionary contingency. [Biotic seed dispersal; contingency; C_4 photosynthesis; diversification; eyes; key innovation; key trait; predictability.]

A fundamental question in evolutionary biology is, "Why have certain groups diversified more than others?" A traditional answer to this question invokes the idea of a key innovation: Exceptionally diverse groups possess some trait or set of traits that promotes diversification (Miller, 1949; Simpson, 1953). However, beginning in the 1970s, the importance of such key traits has been questioned on several fronts. First, computer simulations showed that a process of random speciation and extinction could produce strong variation in the numbers of species contained in clades of equal age (Raup et al., 1973; Gould et al., 1977; Slowinski, 1990). This finding undermined the assumption that very diverse groups necessarily require a deterministic explanation. Second, it was recognized that most key innovation arguments were based only on plausibility, without any clear testing of hypotheses (Cracraft, 1990).

Despite these legitimate criticisms, evolutionary biologists as a whole never abandoned the idea of key innovations, and within the last 15 years, both of the above criticisms have been addressed in certain cases. Regarding the first point, several studies have shown that real phylogenies tend to be more unbalanced than would be expected under a random speciation/extinction process (Guyer and Slowinski, 1991, 1993; Heard, 1992; Mooers, 1995; Purvis and Agapow, 2002; but see Savage, 1983), which is

at least consistent with the idea that key traits have influenced diversification. Regarding the second point, tests involving multiple origins of particular traits have shown that some traits are significantly associated with increased diversification (e.g., phytophagy in insects: Mitter et al., 1988; latex and resin canals in plants: Farrell et al., 1991; nectar spurs in angiosperms: Hodges and Arnold, 1995). A few tests of mechanisms of increased diversification also have been performed. For example, Fulton and Hodges (1999) showed that variation in nectar spur length in columbines altered the effectiveness of pollination by hawkmoths, thus providing a potential link between nectar spurs and reproductive isolation. These various studies have refocused attention on the idea of key innovations by demonstrating the feasibility of testing key innovation hypotheses (for recent reviews see Erwin, 1992; Heard and Hauser, 1995; Hunter, 1998; Schluter, 2000).

Despite these advances, there are still relatively few convincing examples of traits that have consistently spurred diversification. The paucity of such cases may reflect a lack of study. However, it might also reflect real deterministic differences in the effect of a particular trait on diversification among clades, times, and places (Sanderson and Donoghue, 1994, 1996; Brown, 1995; Heard and Hauser, 1995). Such differences might

obscure consistent but context-dependent connections between traits and diversification. However, just as one can test whether a trait is a key innovation in general, it is also possible to test deterministic hypotheses to explain the differential effect of a trait on diversification in different contexts. In statistical terms, this amounts to testing for an interaction between the effects of the key trait and other factors. Here, I discuss several studies that represent tests of this sort. Because there are few relevant, definitive studies, my aim is largely to demonstrate, mostly by example, that this area of study is *potentially* rich.

The context-dependence of a trait's effect on diversification relates to contingency in evolution, the idea that evolutionary events are dependent on the specific and largely unpredictable events that precede them (Gould, 1989). Whether one views contingency as a profound insight or a truism, it seems clear that the nature of contingency in evolution is poorly understood, perhaps especially as it relates to macroevolution. Thus, I also discuss some implications of the examples below for the broad issue of evolutionary contingency.

SOME ISSUES OF SCOPE

This paper deals with particular traits that may promote diversification but that are not necessarily innovations, i.e., novelties, in the usual sense. Specifically, a trait might exist for some time (perhaps a very long time) without promoting diversification but, with a change of context, subsequently act to increase diversification. In other words, when the trait begins to promote diversification, it might no longer be an innovation. One might think of the combination of trait and new context as constituting the key innovation, but it seems less confusing to dispense with the word innovation in such cases and simply talk about key traits. (However, I sometimes use "innovation" when the trait in question is newly evolved.)

The meaning and/or the measure of evolutionary diversification varies somewhat among the cases presented. For most of these cases, the key trait hypothesis predicts an increase in net speciation rate (speciation minus extinction). This rate may be measured either directly through changes in species numbers or indirectly through changes in numbers of taxa at some higher rank. In some cases (as in the example of image-forming eyes), the key trait hypothesis predicts an increase in functional diversity as well. In those cases, diversity is still measured taxonomically, and it is assumed that taxonomic diversity reflects functional diversity, a plausible but largely untested assumption (Schluter, 2000).

Heard and Hauser (1995) noted that tests of key innovation hypotheses are of two kinds: tests of the mechanism purported to increase diversification and comparative tests of the predicted correlation between the origin of the trait and increased diversification. The same can be said for hypotheses to explain why a trait's effect on diversification might vary among contexts. Here, I focus on tests of the predicted evolutionary correlation (but see the examples of physical factors). However, as noted by Heard and Hauser (1995), in some cases these tests cast light on mechanisms of diversification, as in the examples of image-forming eyes and biotic seed dispersal.

THREE FACTORS

There are many potential factors that could influence how a trait affects diversification. These factors can be categorized in a very general and preliminary way into three types:

1. Other taxa. Competitive, predator–prey, host–parasite, or mutualistic relationships might determine the extent to which a trait promotes diversification. For example, a trait that allows more effective utilization of particular kinds of prey will only promote diversification if those prey are present.
2. Other traits of the same organisms. The trait in question might only promote diversification in combination with other traits of the taxon of interest. This could apply to traits that function together to make up a more inclusive trait (e.g., the parts making up an eye or a wing), or to traits that function independently in an anatomical or physiological sense but interact ecologically.
3. The physical environment. A trait might only promote diversification in certain physical contexts. Within this category, some obvious potential influences on diversification are climate, topography,

and the chemical composition of the environment.

I present three examples representing these categories. The first example is new and is thus described in much greater detail than the others.

INTERACTIONS AMONG TAXA: ANIMALS WITH IMAGE-FORMING EYES

Interactions among taxa are commonly invoked to explain both the diversification and extinction of groups. In some cases, the influence of such interactions on the diversifying effect of key traits has been considered. For example, evolutionary modifications of the jaws of snakes increased the range of prey that could be ingested (Gans, 1961; Greene, 1997), but this modification may not have spurred diversification until appropriate prey, e.g., rodents, passerine birds, and frogs, had become abundant (Stanley, 1990). Here, I present a new example illustrating how interactions among taxa might influence a trait's effect on diversification.

Various biologists have suggested that the evolution of eyes capable of forming images may promote diversification (Land and Fernald, 1992; Zuker, 1994; Parker, 1995), probably through entrance into a new adaptive zone (sensu Simpson, 1953). Comparisons of species numbers for groups with imaging eyes and their sister groups indicate no significant association between such eyes and diversity, thus failing to support the key innovation hypothesis (de Queiroz, 1999). However, if a key innovation involves entrance into a new adaptive zone, groups that evolve the trait relatively early might diversify widely and then dampen the diversification of groups acquiring the trait later on. In other words, one might expect an interaction between the trait and the existence of other groups that have the trait (Heard and Hauser, 1995).

Processes by which vision could promote the initial diversification in a new adaptive zone have been described elsewhere (de Queiroz, 1999). I focus here on a two-part hypothesis describing how early groups, once they have radiated, might competitively dampen the diversification of later groups. First, the early groups will fill many visual niches and thereby decrease the probability of later groups using those same niches. This effect will be especially strong if members of a species already occupying a niche (incumbents) tend to have an advantage over others that might displace them (Rosenzweig and McCord, 1991). However, the dampening will still occur as long as incumbent species sometimes exclude others from occupying the same niche. Second, members of early evolving groups will be more likely to fill new visual niches. This second effect would result from early groups having had more time to evolve certain correlates of acute vision, such as the neural circuitry for complex coordination of vision and locomotion (Nilsson and Osorio, 1997; Lacalli, 2001), that might allow expansion into an especially large number of new niches. (In this case, one might think of the effect of vision being contingent on other traits of the same organisms, i.e., factor 2 above. However, time of origin in relation to other groups would still be the ultimate cause of the pattern.) One can think of the early groups as usually winning the race into a new niche before later groups even get out of the starting blocks.

This two-part dampening hypothesis involves competitive exclusion of later groups from visual niches. In general, the victims of the process would not be entire species but rather individuals that vary in the direction of members of the early evolving groups. A troubling point is that the hypothesis assumes the existence of one or more visual adaptive zones that apply to very disparate taxa such as vertebrates and scallops. Active predation and/or active escape from visual predators might be features partly defining such zones; imaging eyes are significantly associated with mobility (de Queiroz, 1999). Nonetheless, the assumption of common adaptive zones will probably be considered untenable by some.

In evaluating this hypothesis, I begin with a simple observation and then see how that observation stands up to some (limited) refinement. The observation is that the first 3 groups known to have evolved image-forming eyes—the arthropods, vertebrates, and cephalopod molluscs—have each contained, at various times, at least dozens of families and thousands of species, whereas none of at least 15 groups that later evolved such eyes have diversified to anything like that extent (Benton, 1993; de Queiroz, 1999, and references therein). The maximum

number of contemporaneous families for any of these later groups is eight, and most have never attained diversities of more than four contemporaneous families (Benton, 1993).

An obvious potential confounding factor is that the first three groups have had longer to diversify than have the later-evolving groups. Here, I describe an analysis using only the eight groups with a good fossil record, in which I addressed this problem in a quantitative but rough way by comparing diversities for only the first approximately 88 million years (MY) of each group's existence. This time span was chosen because it is the estimated age of the youngest visual group and thus provided the longest possible window for measuring diversity that allowed all groups to be included in the analysis. The window was measured from the midpoint of the stage/epoch of first appearance to the midpoint of the stage/epoch that gave a window length as close to 88 MY as possible. The range of window lengths was 84–92 MY.

Fossil first appearances were taken from Benton (1993), and origination times were calculated as the midpoint of the stage or epoch in question. (The use of both stages and epochs was dictated by Benton's use of these different classes of time periods for different parts of the geological record. However, this differential use was appropriate because it subdivided the record into intervals of more similar length than would otherwise have been the case.) In Benton's compilation, the first appearances of arthropods and vertebrates were localized only to the level of a very long epoch (36 MY). Thus, in the present study, arthropod and vertebrate first appearances were taken from Crimes (1992) and Shu et al. (1999), respectively, and were localized to the level of stage. I used estimates of Young and Laurie (1996) for ages of geological stages and epochs. Some assumptions regarding the circumscription of visual groups are given in the Appendix.

Diversity for each taxon was taken from Benton (1993) and was calculated as the mean number of families per geological stage/epoch over the time window. The family level was chosen primarily because this is the level at which Benton's compilation was done. In addition, the hypothesized dampening of diversification imposed by early groups on later groups might be expected to act most strongly on diversification of func-

tion, and functional diversity might be better reflected by number of families than number of species. Also, the number of families in fossil data is probably far less sensitive to sampling biases than are numbers of species or genera (Foote and Sepkoski, 1999; Benton et al., 2000).

The number of geological stages or epochs encompassed by the first 88 MY of a taxon's existence varied among taxa (from 8 to 18). I performed one set of analyses after standardizing the number of stages/epochs. However, results using standardized and unstandardized data were virtually identical; thus, I present only the unstandardized results.

I evaluated the relationship between diversification and order of origin using a Mann–Whitney test in which the two diversification categories were major and minor evolutionary radiations. Groups were characterized as minor or major radiations based on obvious gaps in the distribution of the mean number of families. There were two such gaps (Fig. 1), one separating arthropods from all other taxa and one separating arthropods, cephalopods, and vertebrates from all other taxa. I report results from analyses using both of these categorizations. The null hypothesis is that there is no difference in order of origin for major and minor radiations. Although categorizing each radiation as major or minor sacrifices some information, the scale of the question and the crudeness of the diversity measure perhaps makes such a categorization more appropriate than the use of the raw diversity data. In any case, an exponential regression using the raw data gave results very similar to those reported below.

When arthropods, cephalopods, and vertebrates are considered the three major radiations of visual animals, then major radiations occurred significantly earlier than minor radiations (Fig. 1; Mann–Whitney test: $U = 15$, $P = 0.036$, two-tailed). When only arthropods are considered a major radiation, the difference is not significant, although the result is as extreme as it can be ($U = 7$, $P = 0.25$, two-tailed).

Comparisons of sister groups are problematic in this case because of lack of information on phylogenetic relationships (e.g., for heteropods and strombids) or poor fossil records of sister groups (e.g., for cephalochordates, the living sister group of vertebrates). However, in the first 88 MY of their existence, arthropods, vertebrates, and cephalopods
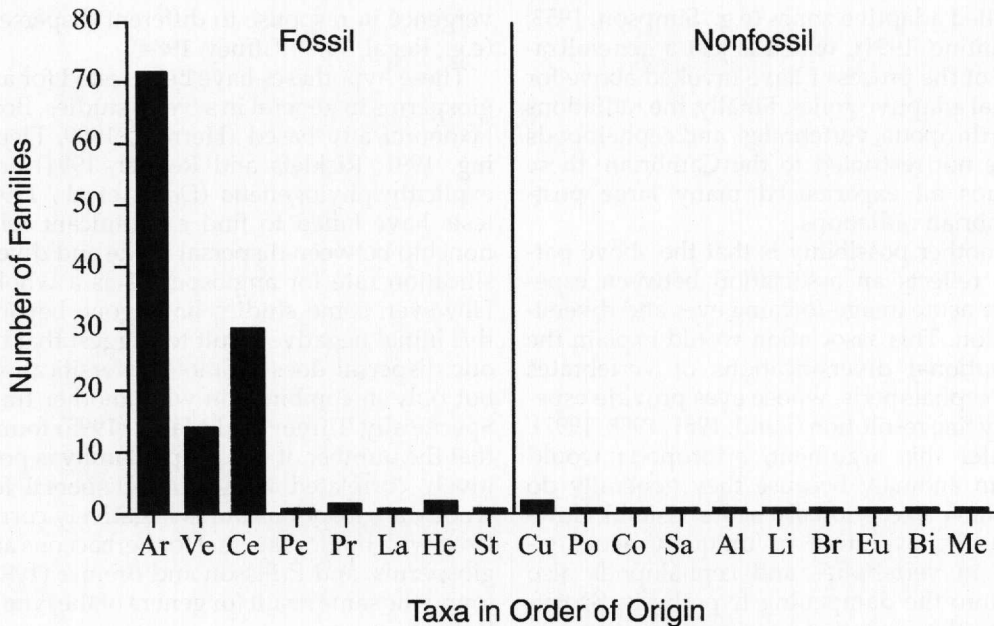
FIGURE 1.   Number of families plotted against order of origin for groups that have independently evolved image-forming eyes. For groups with relatively continuous fossil records, the value is the mean number of families for the first ~88 MY of the group's existence, and the order of origin reflects fossil first appearances. For groups without continuous fossil records, the value is the current number of families. Order of origin for the latter is arbitrary, except that Cubozoa is placed first because members of this group are known from the Pennsylvanian (Foster, 1979), almost undoubtedly predating any of the other groups with poor fossil records. With the possible (but unlikely) exception of Cubozoa, the groups with poor fossil records all originated after the arthropods, vertebrates, and cephalopods. Ar = arthropods; Ve = vertebrates; Ce = cephalopods; Pe = pectinacean bivalves; Pr = prionodontan bivalves; La = laternulid bivalves; He = heteropod gastropods; St = strombid gastropods; Cu = cubozoan cnidarians; Po = pontellid copepods; Co = corycaeid copepods; Sa = sapphirinid copepods; Al = alciopid polychaetes; Li = littorinid gastropods (in part); Br = *Branchiomma* sabellid polychates; Eu = *Eudistylia, Pseudopotamilla,* and *Schizobranchia* sabellid polychaetes; Bi = *Bispira* sabellid polychaetes; Me = *Megalomma* sabellid polychaetes.

were almost certainly more diverse than their sister groups. (The living sister group of cephalopods, the gastropods, is currently more diverse than the cephalopods, but this relationship was reversed in the early history of these groups [Benton, 1993]).

As with the initial observation, the above refinements seem to support the hypothesis that diversification depends on whether other groups have already evolved imaging eyes. However, the data are strongly phylogenetically biased in that the five clades that evolved imaging eyes most recently are all molluscs. Thus, one might argue that the pattern simply reflects the peculiar inability of molluscs (other than cephalopods) to radiate into visual niches. However, the later visual groups without good fossil records include diverse metazoan taxa (e.g., cnidarians, annelids, and crustaceans that lost and re-evolved good vision; Fig. 1), and at least

some of these groups (e.g., cubozoan cnidarians and alciopid polychaetes) probably have existed for many millions of years without diversifying widely. In other words, the pattern does seem to hold for nonmolluscan taxa and would almost undoubtedly be strengthened if these groups had reasonable fossil records.

There are other possible explanations of the relationship between diversification and order of origin. The early, rapid diversifications of the arthropods, vertebrates, and cephalopods all took place partly in the Cambrian and thus might be explained by whatever caused the Cambrian explosion in general (e.g., Gould, 1989; Knoll and Carroll, 1999). There are several responses to this argument. First, there is debate about whether the Cambrian really was a period of exceptionally rapid diversification (e.g., Smith, 1988; Lieberman, 2001). Second, Cambrian radiations might represent expansion into

unfilled adaptive zones (e.g., Simpson, 1953; Valentine, 1991), which is just a generalization of the process I have invoked above for visual adaptive zones. Finally, the radiations of arthropods, vertebrates, and cephalopods were not restricted to the Cambrian; these groups all experienced many large post-Cambrian radiations.

Another possibility is that the above pattern reflects an association between especially acute image-forming eyes and diversification. This association would explain the exceptional diversifications of vertebrates and cephalopods, whose eyes provide especially fine resolution (Land, 1981, 1988, 1997). (Under this argument, arthropods would be an anomaly because they generally do not have exceptionally acute vision.) However, the evolution of uniquely acute vision in vertebrates and cephalopods also fits into the dampening hypothesis. Specifically, the evolution of exceptionally acute vision in these groups may have prevented later visual groups from evolving in that direction.

In summary, the temporal pattern of diversification described above is consistent with the idea that the diversifying effect of image-forming eyes in particular groups was strongly influenced by the existence of other animals with such eyes. This example also illustrates how a pattern of contingency can itself discriminate between alternative hypothesized mechanisms of diversification (Heard and Hauser, 1995). In particular, the relationship between diversity and order of origin is predicted by the mechanism of entrance into a new adaptive zone but not by some other mechanisms, e.g., increased opportunities for reproductive isolation through the use of a new or altered sensory modality (Ryan, 1986).

EFFECTS OF OTHER TRAITS: BIOTIC SEED
DISPERSAL AND GROWTH FORM
IN FLOWERING PLANTS

The influence of one trait on another trait's effect on diversification is perhaps best exemplified by studies of the effect of seed dispersal mode on angiosperm diversification. The initial idea was that the evolution of biotic seed dispersal should increase speciation rate by limiting dispersal abilities (e.g., Tiffney, 1984) and/or promoting adaptive divergence in response to different dispersers (e.g., Regal, 1977; Tiffney, 1984).

These hypotheses have been tested for angiosperms in general in several studies. Both taxonomically based (Herrera, 1989; Fleming, 1991; Ricklefs and Renner, 1994) and explicitly phylogenetic (Dodd et al., 1999) tests have failed to find a significant relationship between dispersal mode and diversification rate for angiosperms as a whole. However, some studies have gone beyond this initial negative result to suggest that biotic dispersal does promote diversification, but only in combination with another trait. Specifically, Tiffney and Mazer (1995) found that the number of species per family is positively correlated with biotic dispersal for woody angiosperms but is negatively correlated with biotic dispersal for herbaceous angiosperms, and Eriksson and Bremer (1991) found the same result for genera of the family Rubiaceae.

Tiffney and Mazer (1995) suggested that large seed size is often required of woody plants because such plants create a low-light environment for germination. They argued that for large-seeded plants dispersal away from the parent plant (which is advantageous for several reasons) is most effectively achieved by animal dispersers. The advantage of animal dispersal for large-seeded plants leads to reduced extinction rates, thus producing the observed positive correlation between biotic dispersal and net speciation for woody plants.

Dodd et al. (1999) criticized earlier studies of angiosperm diversification on the grounds of lack of phylogenetic independence of data points, among other things. Dodd et al.'s own explicitly phylogenetic analyses did not show significant effects of dispersal mode on diversification for either woody or herbaceous groups. However, a simple analysis of Dodd et al.'s data does show a significant interaction between biotic dispersal and growth form on diversification (Fig. 2). Thus, Dodd et al.'s data do not support the idea that animal dispersal produces higher diversification rates for woody plants but do confirm that the effect of dispersal mode is contingent on growth form (or some factor related to growth form, such as seed size).

For my purposes, the main point of these studies is that the effect of dispersal mode on diversification appears to be contingent on whether the group in question is woody
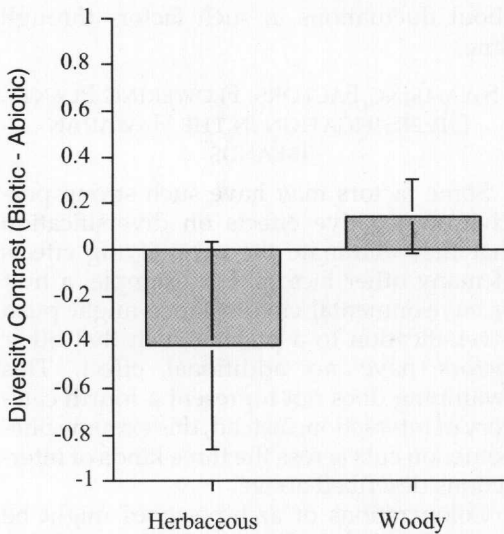
FIGURE 2. Comparisons of species diversity for angiosperm sister taxa with biotic versus abiotic seed dispersal. Bars indicate the mean standardized contrast of the $\log_{10}$ of species number. A positive value indicates that the biotically dispersed clades tend to be more diverse than their sister groups; a negative value indicates that the biotically dispersed clades tend to be less diverse. Lines indicate ± 2 SE. Data (standardized contrasts) were taken from Dodd et al. (1999). The mean standardized contrasts for woody and herbaceous plants do not differ significantly from zero. However, the mean standardized contrast for herbaceous plants differs significantly from that for woody plants ($T = -2.896$, df = 36, $P < 0.01$), indicating that the correlation between biotic dispersal and diversity is dependent on growth form (or some trait correlated with growth form).

or herbaceous (possibly because of differences in seed size between plants with these growth forms). This may be the clearest published example suggesting that a key trait only acts as such in combination with some other trait. This contingency has led to a reconsideration of the mechanism of increased diversification. Initially, the proposed mechanism involved increased speciation through higher rates of isolation and/or adaptive divergence. However, the restriction of the positive effect of biotic dispersal to woody plants has focused attention on a mechanism involving reduced extinction due to enhanced competitive abilities (Tiffney and Mazer, 1995; but see Smith, 2001). Thus, as in the case of image-forming eyes, the demonstration of contingency has ramifications for evaluating mechanisms of diversification.

THE PHYSICAL ENVIRONMENT: C_4 PLANTS AND ATMOSPHERIC CO_2 LEVELS

It seems obvious that physical factors can influence diversification. For example, climate change has frequently been invoked to explain the proliferation or demise of groups (e.g., Vrba, 1995; Garcia-Pichel, 1998). However, few such cases make explicit links among physical factors, diversification, and a key trait.

The main example I use here involves the effect of atmospheric CO_2 levels on the diversification of plants that use C_4 photosynthesis. C_4 plants use a biochemical carbon pump to raise CO_2 concentrations in bundle sheath cells (where Rubisco-catalyzed carbon fixation occurs) as much as 10-fold over ambient levels. This process carries a cost but also increases efficiency of the Rubisco-catalyzed reaction because it reduces photorespiration. Under relatively low levels of atmospheric CO_2 (and high temperatures), this increase in efficiency is particularly strong and can more than offset the cost (Ehleringer et al., 1991; Ehleringer and Monson, 1993). In short, the photosynthetic efficiency of C_4 plants compared with C_3 plants is dependent on atmospheric CO_2 levels.

Photosynthetic efficiency can translate into competitive ability (Carter and Peterson, 1983; Bazzaz and Carlson, 1984), which provides a potential link to diversification. Increased competitive abilities could directly increase the probability of a species' survival by increasing the probability that individual plants will survive. Enhanced competitive abilities might also lead to species having larger geographic ranges, which could decrease the probability of stochastic extinction (Pimm et al., 1988). These arguments suggest that the evolutionary diversification of C_4 plants should be tied to CO_2 levels.

This prediction is complicated by the fact that C_4 monocots have significantly more efficient photosynthesis than do C_4 dicots, perhaps because of differences in leaf venation patterns (Ehleringer et al., 1997). Furthermore, arguments for the efficiency of the C_4 pathway predict that the abundance of C_4 plants should be strongly positively correlated with temperature, but empirically this hypothesis is supported only for C_4 monocots, not C_4 dicots (Stowe and Teeri, 1978). These results suggest that C_4 photosynthesis may act as a key trait only for monocots.

Evidence of the expected evolutionary pattern is sketchy. According to the photosynthesis calculations of Sage (2001), atmospheric CO_2 reached a level low enough to favor C_4 plants in some habitats approximately 30 MY ago (MYA). Although C_4 monocots probably existed more than 25 MYA (Kellogg, 1999), C_4 plants did not become major components of ecosystems until about 7 MYA (Quade et al., 1989; Cerling et al., 1997), which might seem to refute the hypothesized connection between the diversification of C_4 plants and CO_2. However, the atmospheric CO_2 level 7 MYA was probably much lower than that at 30 MYA (Berner, 1994), thus one can still argue that CO_2 level was critical for the proliferation of C_4 plants. On a finer time scale, CO_2 levels were lower during the last glacial period than they are today, and C_4 plants seem to have been more prevalent during that time (Ehleringer et al., 1997).

These possible correlations between CO_2 and C_4 plants are based on measures of the overall production of carbon by C_4 plants, not on measures of species diversity. Thus, to link CO_2 to evolutionary diversification, one must assume that overall productivity is related to species diversity. What is needed is a direct assessment of the relative diversification rates of the various independently evolved C_4 monocots and their C_3 relatives at times of differing CO_2 concentrations. At present, the case of C_4 plants provides a plausible mechanism of diversification in need of verification of the expected evolutionary pattern.

Some other suggested examples of the dependence of key traits on physical factors also seem plausible but lack strong support for the expected pattern of diversification. For example, Marcotte (1999) argued that the diversification of visually oriented aquatic animals has been influenced by levels of turbidity in the oceans, but provided no general, quantitative evaluation of the expected pattern. Similarly, Dudley (2000) suggested that high atmospheric O_2 levels promoted the origins and radiations of flying animals by facilitating aerodynamic lift and the maintenance of high metabolic rates, but he gave only weak evidence of the expected evolutionary correlation. The influence of the above and other physical factors on the effect of key traits may become more apparent with increasingly precise information about fluctuations in such factors through time.

SWAMPING FACTORS: FLOWERING PLANT DIVERSIFICATION IN THE HAWAIIAN ISLANDS

Some factors may have such strong positive or negative effects on diversification that they eliminate the diversifying effects of many other factors. For example, a trait or environmental circumstance might push diversification to a plateau such that other factors have no additional effect. This swamping does not represent a fourth category of interaction; instead, this extreme phenomenon cuts across the three kinds of interactions described above.

Colonizations of archipelagoes might be especially likely to produce such swamping through a combination of increased opportunities for geographic isolation and radiation into empty niches (Lack, 1947; Schluter, 2000). These effects on diversification might be so strong that they eliminate the effects of traits that under other circumstances would promote diversification. In other words, the effect of a key trait might be contingent on whether the group in question finds itself in an archipelago.

A hint at this kind of contingency comes from a study of flowering plant diversification in the Hawaiian Islands. Ricklefs and Renner (2000) tested for correlations between the logarithm of number of species and various factors for 265 independent angiosperm colonization events in the Hawaiian archipelago. In previous analyses of angiosperms in general (Ricklefs and Renner, 1994), they had found that biotic pollination and herbaceous growth form were positively related to diversity. These earlier analyses also showed that taxa with both biotic and abiotic dispersal or with both woody and herbaceous growth forms tended to be more diverse than taxa with only one dispersal mode or growth form. In contrast, diversity in Hawaiian lineages was unrelated to any of these factors except pollination mode. Ricklefs and Renner (2000:1064) suggested that the "propensity for adaptive radiation of lineages within the Hawaiian Islands is generally unrelated... to character traits possessed by the larger monophyletic group to which the colonists belong." Their results are at least consistent with the idea that archipelago effects spurred diversification so

strongly that the typical influences of certain traits on diversity were not seen.

A possible problem is that Ricklefs and Renner (2000) did not account for different ages of Hawaiian colonization events; variable ages may have obscured real correlations for Hawaiian taxa. Also, even if one accepts their results, my interpretation that exceptionally strong archipelago effects have swamped out other factors does not necessarily follow. Although there is evidence that net speciation rates of plants have accelerated in Hawaii (Baldwin and Sanderson, 1998; Schluter, 2000), it is unclear whether the rates have reached a plateau, as is predicted by the swamping hypothesis. This example is presented to illustrate the possibility of swamping, not as a convincing case.

ANALYTICAL PROBLEMS

A major goal of this paper is to illustrate the broad range of factors that might influence a particular trait's effect on diversification. Such factors may be so pervasive that they have obscured the diversifying effects of many key traits. A practical message here is that the failure to find an overall correlation between some trait and enhanced diversification should not be considered the end of a key trait study (see the examples of image-forming eyes and biotic seed dispersal). Some key traits (e.g., phytophagy, flight, nectar spurs) may have fairly consistent effects, but these cases may be relatively rare. We need to explore more complex hypotheses such as those described here to fully understand the role of key traits in evolutionary diversification.

Figure 3 illustrates some of these more complex key trait hypotheses. Further interactions can easily be imagined. For example, the effect of a trait might depend both on other traits and on some environmental variable. That kind of relationship has been suggested for C_4 photosynthesis, which may be especially advantageous only in combination with particular leaf venation patterns and low CO_2 levels.

Testing contingent key trait hypotheses presents problems beyond those encountered when only one factor (the key trait) is considered. First, hypotheses involving factors to which all lineages are simultaneously subjected (as in Fig. 3a) will generally require information about the absolute tim-
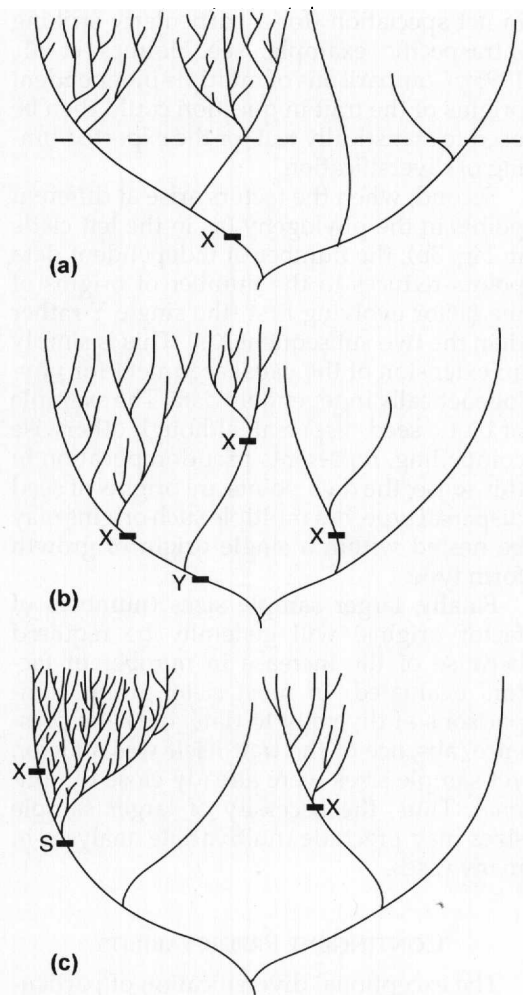

FIGURE 3. Three idealized scenarios for the contingent nature of the diversifying effect of key traits. (a) The positive effect of key trait X is dependent on biotic or abiotic conditions that become prevalent at the time indicated by the dashed line. The idea that the diversification of C_4 plants is connected to relatively low CO_2 levels fits this scenario. (b) The positive effect of trait X is dependent on the existence of trait Y. The hypothesized connection among biotic seed dispersal, woody growth habit, and diversification is a possible example. (c) Trait or condition S (the swamping factor) causes such a strong increase in diversification that it eliminates the diversifying effect of trait X. Radiations of angiosperms in the Hawaiian Islands, where S represents an archipelago effect, might be a case of this sort.

ing of radiations. Such information could come from the fossil record and associated radiometric dates or from molecular data (appropriately calibrated). Plots of lineages through time estimated from molecular phylogenies of extant species (Harvey et al., 1994) might be used to show temporal variation

in net speciation (for a particularly striking intraspecific example, see Holmes et al., 1995). Comparisons of multiple independent origins of the trait in question could then be used to statistically test for the expected timing of diversification.

Second, when the factors arise at different points in the phylogeny (as in the left clade in Fig. 3b), the number of independent data points reduces to the number of origins of the factor evolving first (the single Y rather than the two subsequent X's). This is simply an extension of the usual argument for phylogenetically independent data. The example of biotic seed dispersal, although otherwise compelling, represents pseudoreplication in this sense; the data points are origins of seed dispersal type, but multiple such origins may be nested within a single origin of growth form type.

Finally, larger sample sizes (numbers of factor origins) will generally be required because of the increase in number of factors evaluated. In most sister-group comparisons of diversity to date, only the presence/absence of the trait itself was a factor, yet sample sizes were already close to minimal. Thus, the necessity of larger sample sizes may preclude multivariate analyses in many cases.

CONTINGENT PREDICTABILITY

The exceptional diversification of particular groups has often been viewed as either indecipherable (Cracraft, 1990) or, more usually, due to traits or sets of traits unique to the group in question. For example, some traditional explanations for the striking radiations of the three largest clades of visual animals invoke unique attributes of these taxa, e.g., the jointed exoskeleton of arthropods (Brusca and Brusca, 1990), neural crest tissue and the resulting head structures of vertebrates (Gans and Northcutt, 1983), and the siphuncle (a buoyancy organ) of cephalopods (Runnegar and Pojeta, 1985). In contrast, I propose that exceptional radiations might frequently be ascribable to traits that have arisen multiple times and that show some regular tendency to promote diversification. As has been argued for the convergent evolution of traits (Conway Morris, 1998; Huey et al., 2000) and communities (Losos et al., 1998), such repeated patterns suggest a kind of evolutionary predictability. For example, to twist Gould's (1989) well-known metaphor, if we replayed the tape of angiosperm evolution, we might expect to see some groups of exceptionally diverse, biotically dispersed plants in each replay.

However, these examples also indicate that even these repeated radiations are contingent, i.e., dependent on particular contexts that may themselves be unpredictable. For example, radiations of C_4 plants might be predictable, but only given appropriately low CO_2 levels (and perhaps also first requiring the evolution of monocots). The contingency of key traits illustrates what I suspect is a very general pattern in evolution: many things are repeated and are therefore in some sense predictable, but only in certain contexts. Repeated events that occur predictably only within certain clades—e.g., Cope's rule pertaining to mammals (Alroy, 1998) but not to molluscs (Jablonski, 1997)—are an obvious class of this sort, but, as the key trait examples illustrate, many other kinds of contingencies are possible. In short, evolution probably often shows the property of contingent predictability (see Taylor and McPhail, 2000, for a similar view).

Gould (1989) championed the view that specific evolutionary events or sequences, such as the origin of mammals, are highly contingent. Most evolutionary biologists probably agree with this perspective (see Conway Morris, 1998, for discussion). However, because of the uniqueness of such events, their contingent nature is difficult to evaluate. The examples above differ in that the events have been repeated, thus facilitating statistical testing of hypotheses of contingency. It is ironic that studies of contingency in evolutionary diversification may need to rely on evolutionary repetition; in short, understanding contingency may require a degree of predictability.

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APPENDIX:
JUSTIFICATION OF CIRCUMSCRIPTION OF SOME GROUPS USED IN THE ANALYSIS OF IMAGE-FORMING EYES

The categorization of eyes as image forming (following Land and Fernald, 1992; de Queiroz, 1999) is debatable for some groups, particularly, the prionodontan bivalves and the various groups of sabellid polychaetes (Nilsson, 1994). However, even these ambiguous taxa represent strong evolutionary increases in visual abilities (de Queiroz, 1999). Removal of these taxa does not alter the general pattern, although it does render the quantitative analysis nonsignificant.

I included conodonts as vertebrates with image-forming eyes, a decision that has a major impact on the estimated diversity of this visual group. Recent phylogenetic analyses and anatomical arguments support these contentions (Donoghue et al., 1998, 2000; but see Pridmore et al., 1997).

I assumed that all cephalopods had image-forming eyes. The basal split in the cephalopod crown group is currently represented by *Nautilus* on one side and the dibranchiate coleoids (octopuses, squid, and cuttlefishes) on the other (Engeser, 1990). The coleoids have a well-developed camera-type eye with a lens. *Nautilus* has a pin-hole eye but with accessory structures indicating that adjustment of the image is important to the animal (Hurley et al., 1978; Hartline et al., 1979; Barber, 1987). Thus, I assume that the common ancestor of these taxa minimally had an image-forming pin-hole type eye. Following Engeser's tentative (but apparently synapomorphy-based) phylogeny, this assumption would also hold for the common ancestor of all cephalopods with the possible exception of the Ellesmerocerida. Exclusion of the latter group does not affect the results.

I assumed that image-forming eyes are a synapomorphy for known arthropods. There is debate about whether compound eyes are a synapomorphy for arthropods (e.g., Paulus, 1979; Nilsson, 1989; Osorio and Bacon, 1994). However, I am here assuming only that camera-type and compound image-forming eyes of arthropods are both derived from some kind of imaging eye.