

CHAPTER

7

The Evolution of Biodiversity



Modern biodiversity. Tropical coral reefs are the most species-rich marine environments, harboring hundreds of species. At Apo Island Marine Reserve in the Philippines, the Cogon reefs of soft and hard corals harbor a multitude of species including the sponges, tunicates, feather stars, sea stars, and fish seen here. (Photo © Andre Seale/Photolibary.com.)

Biological diversity, or **biodiversity**, poses some of the most interesting questions in biology. Why are there more species of rodents than of primates, of flowering plants than of ferns? Why do some regions, such as the tropics, have more species than others, such as temperate areas? Why has the diversity of species changed over evolutionary time? Does diversity increase steadily, or has it reached a limit? Because so many factors can influence the diversity of species, these questions are both interesting and challenging.

Biodiversity can be studied from the complementary perspectives of ecology and evolutionary history. Ecologists focus primarily on factors that operate over short time scales to influence diversity within local habitats or regions. But factors that operate on longer time scales, such as climate change and evolution, also affect diversity. On a scale of millions of years, extinction, adaptation, speciation, climate change, and geological change create the potential for entirely different assemblages of species. In this chapter, we will examine long-term patterns of change in diversity, caused by originations and extinctions of taxa on a scale of millions of years. Ecological and evolutionary studies of contemporary species help to interpret these paleontological patterns. Conversely, understanding factors that have altered biodiversity in the past may help us predict how diversity will be affected by current and future environmental changes, such as the global climate change that is now underway as a result of human use of fossil fuels.

Estimating and Modeling Biological Diversity

Estimates of diversity

The simplest expression of taxonomic diversity is a simple count of species (SPECIES RICHNESS). Over long time scales or large areas, species diversity is often estimated by compiling records, such as the publications or museum specimens that have been accumulated by many investigators, into faunal or floral lists of species. Most paleontological studies of diversity employ counts of higher taxa, such as families and genera, because they generally provide a more complete fossil record than individual species do.

Diversity, like almost everything studied by scientists, is estimated from samples. Thus our picture is incomplete, and can often be systematically biased (misleading). Paleobiologists continue to study the effects of sampling on their estimates of diversity (e.g., Alroy et al. 2008), and have developed correction factors that often must be included in data analysis (Raup 1972; Signor 1985; Foote 2000a). For example, rare species are more likely to be included in large than small samples; so the estimated number of species increases with sample size. One way of correcting for this, called *rarefaction*, is to pick the same number of specimens at random from all the samples (perhaps the same number as are in the smallest sample). An important problem in paleontology is that records of fossil taxa are often described at the level of the stages (mostly about 5 to 6 Myr long) into which each geological period is divided. Thus the first and last occurrences of a taxon in the record are accurate only to about 5 Myr, so the estimated duration of the taxon is imprecise. Moreover, geological stages vary in duration, and more recent geological times are represented by greater volumes and areas of fossil-bearing rock. Therefore, it may be necessary to adjust the count of taxa by the amount of time and rock volume represented.

Because fossils are a small sample of the organisms that actually lived, a taxon is often recorded from several separated time horizons, but not from those in between. We therefore can deduce that in the same way, the actual time of origination of a taxon may have occurred before its earliest fossil record, and its extinction after its latest record. It follows that if many taxa actually became extinct in the same time interval, the last recorded occurrences of some are likely to be earlier, so their *apparent* times of extinction will be spread out over time. Conversely, if many taxa actually originated at the same time, some of them may appear to have originated at later times.

Since our count of living (Recent) species is much more complete than our count of past species, taxa that are still alive today have apparently longer durations and lower extinction rates than they would if they had been recorded only as fossils. That is, we can list a living taxon as present throughout the last 10 Myr, let us say, even if its only fossil occurrence was 10 Myr ago. Because the more recently a taxon arose, the more likely it is to still be extant, diversity will seem to increase as we approach the present, a bias called the **pull of the Recent**. This bias can be reduced by counting only fossil occurrences of each taxon and not listing it for time intervals between its last fossil occurrence and the Recent.

Because of unusually favorable preservation conditions or other chance events, a taxon may be recorded from only a single geological stage, even though it lived longer than that. Such "singletons" make up a higher proportion of taxa as the completeness of sampling decreases and therefore bias the sample; moreover, they can create a spurious correlation between rates of origination and extinction because they appear to originate and become extinct in the same time interval. Diversity may be more accurately estimated by ignoring such singletons and counting only those taxa that cross the border from one stage to another.

The rate of change in diversity depends on the rates at which taxa originate and become extinct. Several expressions for such rates have been used in the paleobiological literature. One is simply the number of taxa originating (or becoming extinct) per Myr (or other time unit). The most useful measure is the number of originations (or extinctions) per taxon ("per capita") per unit time (Foote 2000a).

Taxonomic Diversity through the Phanerozoic

The most complete fossil record has been left by marine animals with hard parts (shells or skeletons). Jack Sepkoski (1984, 1993) accomplished the heroic task of compiling data in the paleontological literature on the stratigraphic ranges of more than 4000 marine skeletonized families and 30,000 genera throughout the 542 Myr of the Phanerozoic. Using this database, he plotted the diversity of families throughout the Phanerozoic, in one of the most famous graphs in the literature of paleobiology (Figure 7.1A). The graph shows a rapid increase in the Cambrian and Ordovician, a plateau throughout the rest of the Paleozoic, and a steady, almost fourfold increase throughout the Mesozoic and Cenozoic. This pattern is interrupted by decreases in diversity caused by mass extinction events. The number of genera of skeletonized marine animals shows a similar pattern of change (Figure 7.1B), and diversity seems to have increased on land as well. The number of families of insects shows a steady increase since the Permian (Figure 7.2A), whereas the diversification of flowering plants and of birds and mammals accounts for dramatic increases in the diversity of vascular plants (Figure 7.2B) and of terrestrial vertebrates (Figure 7.2C) after the mid-Cretaceous.

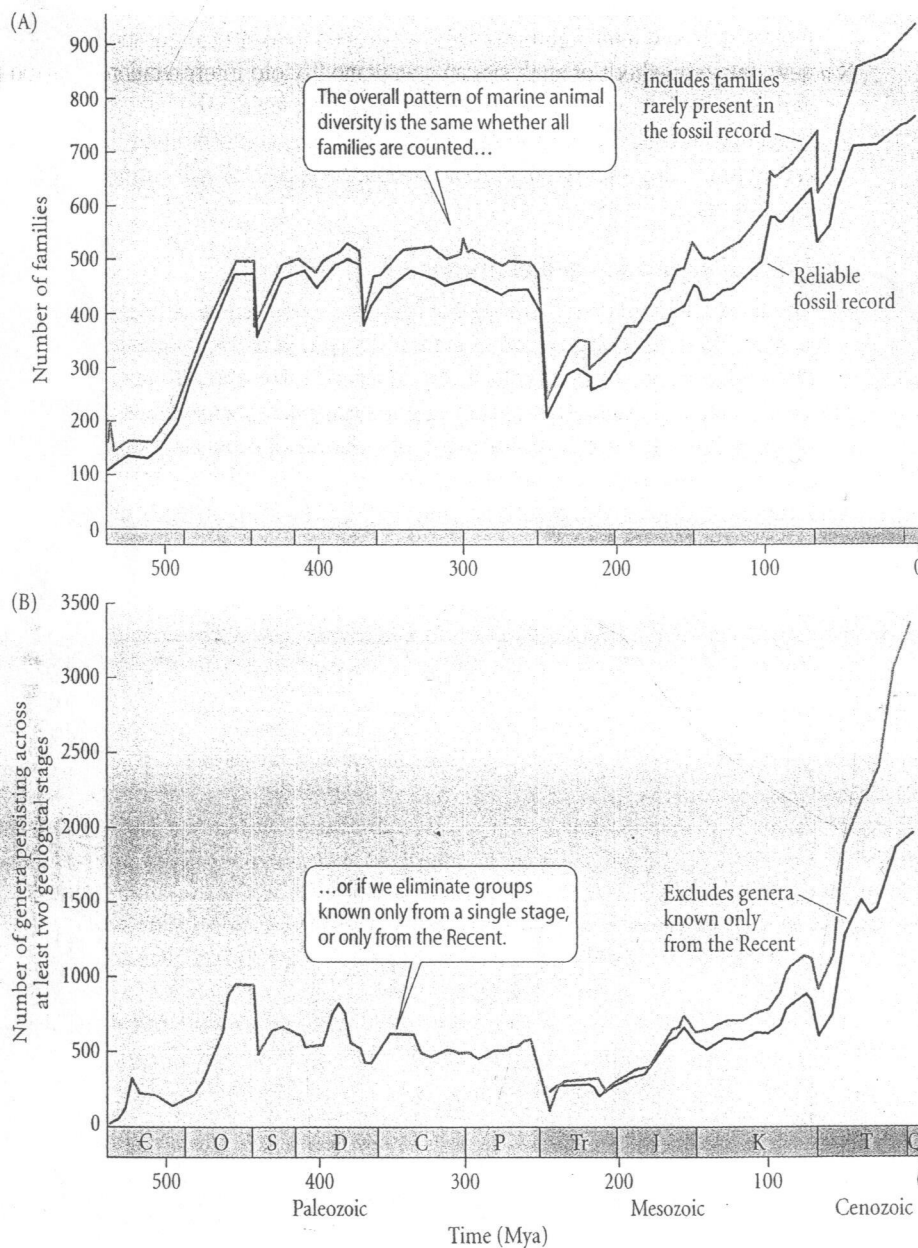


Figure 7.1 (A) Taxonomic diversity of skeletonized marine animal families during the Phanerozoic. The number of taxa entered for each geological stage (subdivisions of the geological periods; most stages represent 5–6 Myr) includes all those whose known temporal extent includes that stage. The blue curve includes families that are rarely preserved; the black curve represents only families that have a more reliable fossil record. There are approximately 1900 marine animal families alive today, including those rarely preserved as fossils. (B) Taxonomic diversity of 25,049 genera of skeletonized marine animals, counting only those that cross boundaries between two or more stages. The lower curve shows genera only as they are represented in the fossil record, excluding their known occurrences in the Recent. (A after Sepkoski 1984; B after Foote 2000a.)

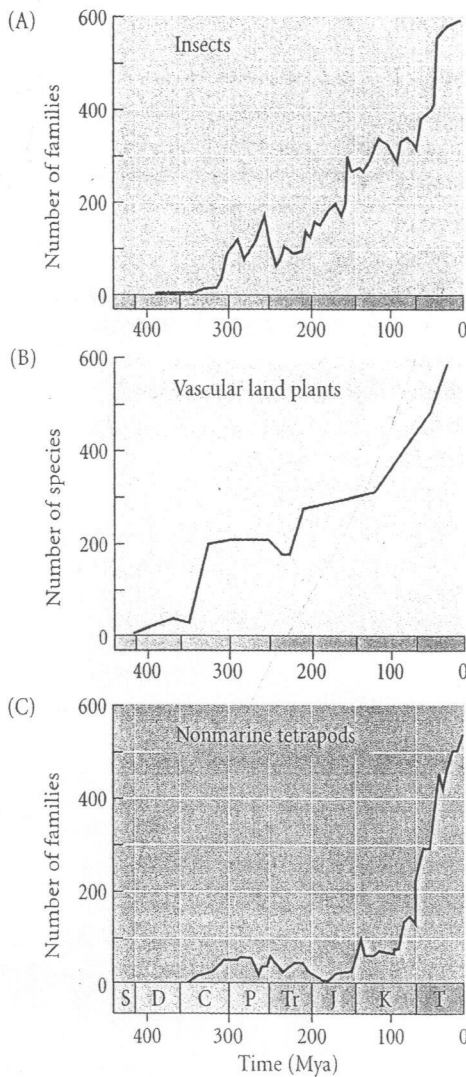


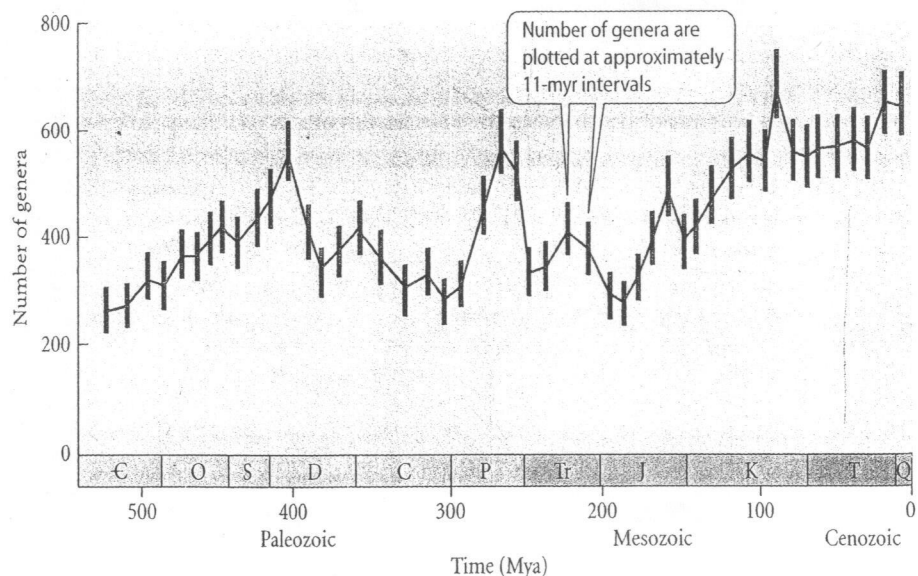
Figure 7.2 Changes in the number of known (A) families of insects, (B) species of vascular land plants, and (C) families of nonmarine tetrapod vertebrates throughout time. (A after Labandeira and Sepkoski 1993; B, C after Benton 1990.)

These plots do not include any of the corrections for sampling errors and biases that we have noted. A large team of researchers has reanalyzed the numbers of marine genera, using a rarefaction procedure on more than 44,000 samples from throughout the Phanerozoic record, as well as several other procedures to minimize systematic errors (Alroy et al. 2008). Their results differ from the Sepkoski plot in several ways (Figure 7.3): there is a decline in diversity in the Devonian instead of a Paleozoic plateau, a sharp increase in the Permian before the end-Permian extinction, and a much less steep post-Paleozoic increase, which seems to have leveled off after the mid-Cretaceous. This analysis has reopened an earlier debate about whether or not to take the pattern in the raw data, especially the dramatic post-Paleozoic increase, at face value. (See Miller 2000 for an intimate history of the debate.) The ongoing struggle to understand the history of biodiversity is a fine example of the way science works: data and interpretations are always open to skeptical questioning, and new data or methods of analysis can always modify old interpretations. It is too early to tell what future research on this subject will yield, whether or not a new consensus will be found, or what other hypotheses about biological diversification (including some described in the following pages) will require rethinking as a result.

Rates of origination and extinction

The increase in diversity during the Mesozoic and Cenozoic tells us that on average, the rate of origination of marine animal taxa has been greater than the rate of extinction, but both rates have fluctuated throughout Phanerozoic history. The rate of origination of new families was highest early in recorded animal evolution, in the Cambrian and Ordovician, and in the early Triassic, after the great end-Permian extinction, but on average, it has declined (Figure 7.4A). Extinction rates have varied dramatically (Figure 7.4B). A distinction is often made between episodes during which exceptionally high numbers of taxa became extinct, the so-called **mass extinctions**, and periods of so-called nor-

Figure 7.3 The number of marine genera through time, corrected for biases such as temporal differences in rock volume and the pull of the Recent. The vertical lines represent the range of values, within which the real number lies. Compare with Figure 7.1B. (After Alroy et al. 2008.)



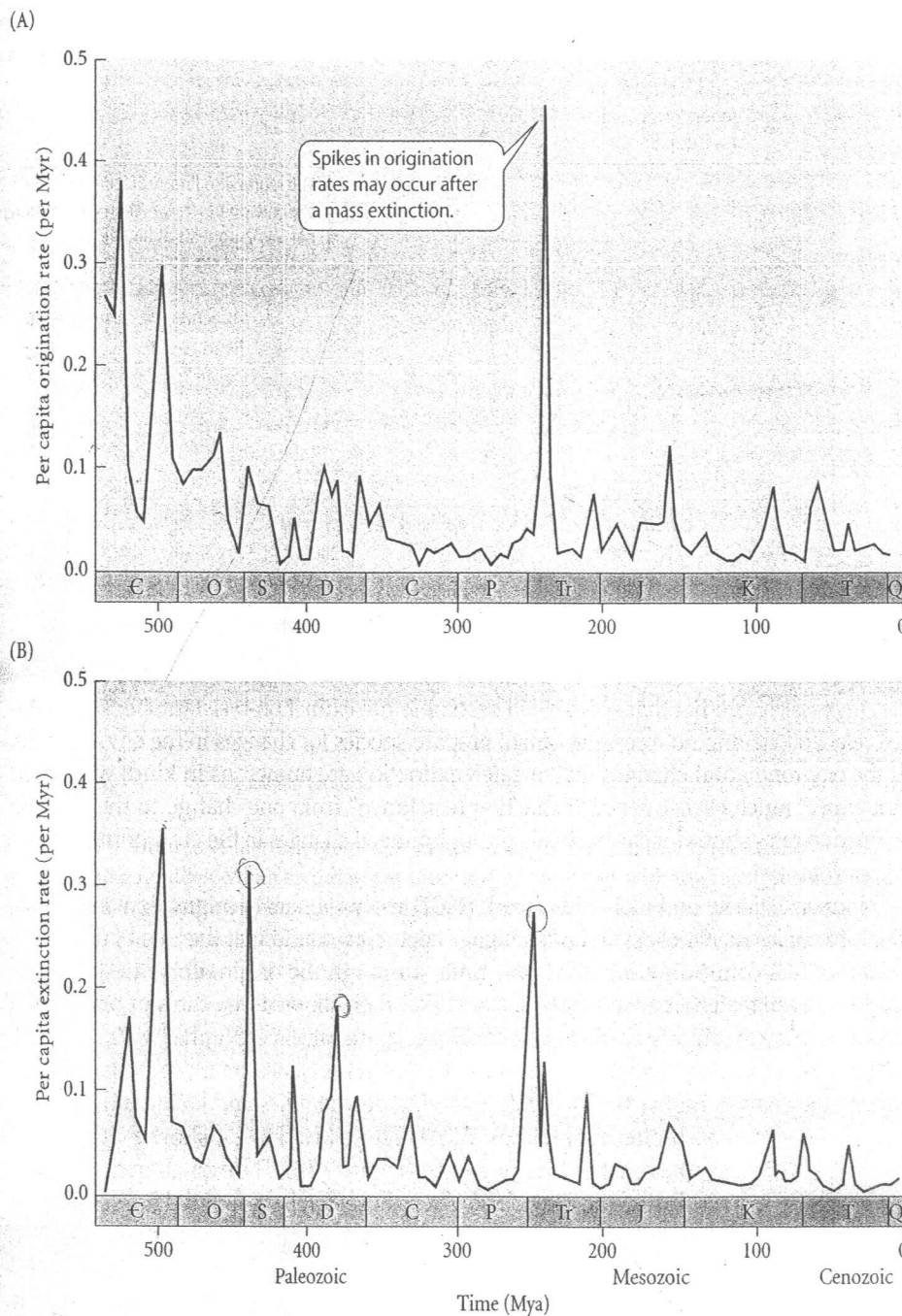


Figure 7.4 Rates of (A) origination and (B) extinction of marine animal genera in 107 stages of the Phanerozoic, expressed as the number of genera per capita per Myr. Only taxa that cross boundaries between stages are counted. Compare the extinction rates with those seen in Figure 7.5, which shows absolute numbers of extinct families, uncorrected for the number that were at risk of extinction at each time. (After Foote 2000a.)

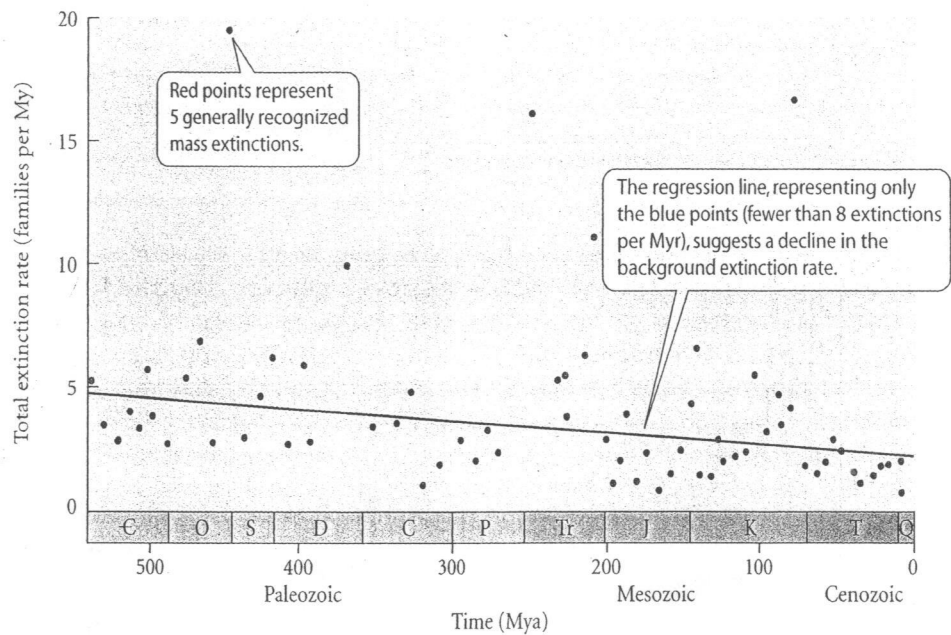
mal or background extinction (Figure 7.5). Five mass extinctions are generally recognized: at the end of the Ordovician, in the late Devonian, at the Permian/Triassic (P/Tr) boundary (the end-Permian extinction), at the end of the Triassic, and at the Cretaceous/Tertiary (K/T) boundary (the K/T extinction). Several other episodes of heightened extinction occurred as well, however. We first discuss background extinction.

Extinction rates have declined over time

David Raup and Jack Sepkoski (1982) discovered that the background extinction rate, scored as absolute numbers of families becoming extinct per Myr, declined during the Phanerozoic (see Figure 7.5). This decline is also seen if extinction rate is measured per capita (see Figure 7.4B). What might account for the decline?

It would seem reasonable to expect lineages of organisms to become more resistant to extinction over the course of time as they become better adapted. However, extinction of species is caused by failure to adapt to environmental changes. Evolutionary theory does

Figure 7.5 Extinction rates of marine animal families during the Phanerozoic, expressed as the number of families per Myr. The solid regression line fits the blue points, which represent fewer than 8 extinctions per Myr. The red points, which deviate significantly from the background cluster, mark the five major mass extinction events at the ends of the (1) Ordovician, (2) Devonian, (3) Permian (the end-Permian extinction), (4) Triassic, and (5) Cretaceous (the K/T extinction). The points in this graph represent absolute numbers of extinctions, not per capita rates, and thus do not control for differences in diversity at different times. (After Raup and Sepkoski 1982.)



not necessarily predict that species will become more extinction-resistant, because natural selection, having no foresight, cannot prepare species for changes in the environment. If the environmental changes that threaten extinction are numerous in kind, we should not expect much carryover of “extinction resistance” from one change to the next. So extinction rates should vary randomly through time, if changes in the environment occur at random.

Norman Gilinsky and Richard Bambach (1987) analyzed rates of origination and extinction of families in 99 orders and other higher taxa. They found that the rate of extinction *within* orders commonly *increased* over time, although the origination rate generally declined even faster (Figure 7.6). Gilinsky (1994) then showed that rates of origination and extinction are highly correlated; for example, both rates were higher in ammonoids and trilobites than in gastropods or bivalves. That is, some clades are more “volatile” than others: they have a higher turnover rate, evolving new families and losing old ones at a higher rate (Figure 7.7A). These taxa have a shorter “life span” before they become extinct (Figure 7.7B). The extinction of such taxa leaves the less volatile taxa, those that have longer “life spans” and lower extinction rates. This process, a form of natural selection among clades (see Chapter 11), results in a decline in the average extinction rate of clades over a long time, as long as highly volatile clades do not evolve anew—which has happened only rarely.

Why are extinction and origination rates correlated? Steven Stanley (1990) suggested that speciation rate may be correlated with extinction rate because both are influenced by certain features of organisms (see also Chapter 18). For these characteristics to deter-

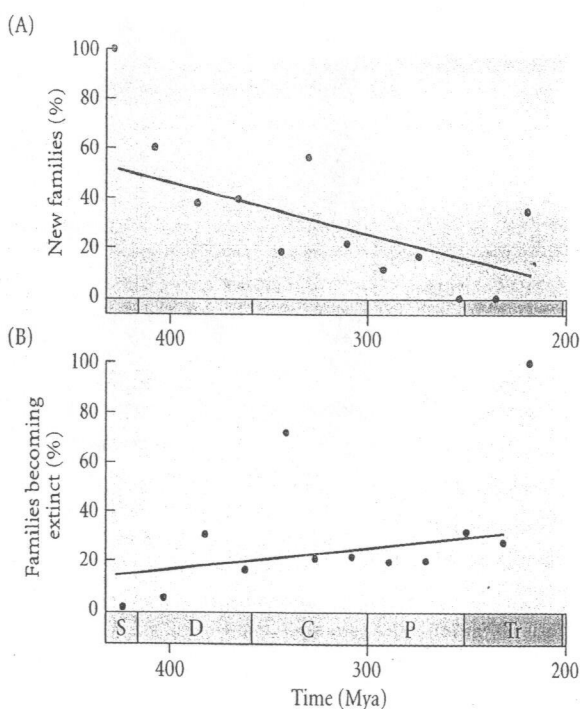


Figure 7.6 Changes in rates of (A) origination and (B) extinction in rugose corals since first appearance of the group. The vertical axis represents the number of families originating or becoming extinct as a percentage of the number of families present at the beginning of the interval. The origination rate declined over time and the extinction rate rose, although at a lower rate. Both effects suggest that as diversity increases, the rate of further increase in diversity (origination–extinction) decreases, so that diversity would tend toward an equilibrium. (After Gilinsky and Bambach 1987.)

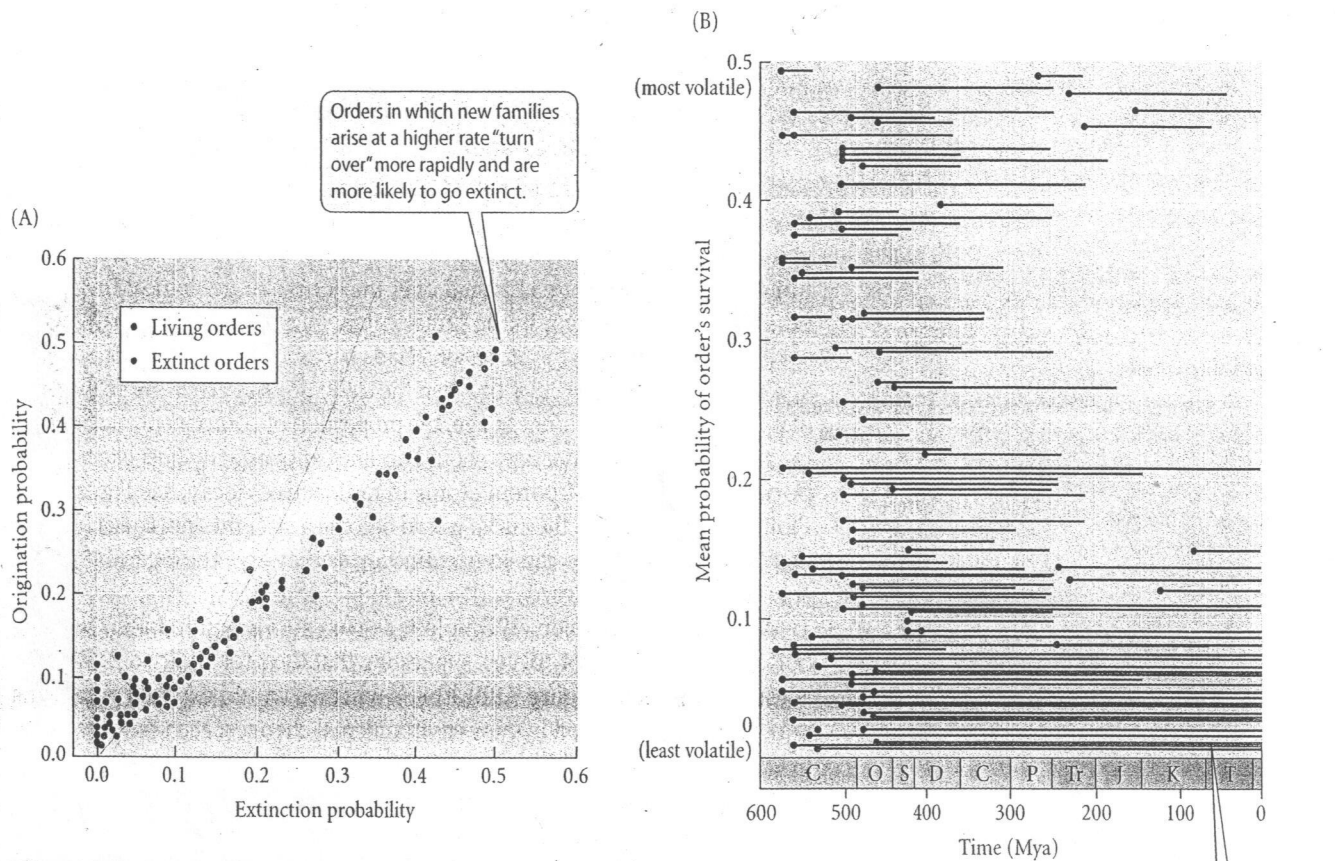


Figure 7.7 Groups of marine organisms vary in volatility. (A) The rate (probability) of origination of new families within an order, per unit time, is correlated with the rate (probability) of extinction. Orders with higher rates have higher turnover, and so are more likely to decrease greatly or become extinct. (B) The temporal duration of each order is plotted as a line extending through geological time (x -axis), in relation to the average of the origination and extinction rates of families within each order (y -axis). Note that the "high" (more volatile) lines are predominantly early in the Phanerozoic (i.e., at left of the diagram); such volatile taxa originated later in geological time. (After Gilinsky 1994.)

mine extinction rates of families, they must be fairly phylogenetically conservative—they should vary consistently among families. Some possible characteristics are:

1. *Degree of ecological specialization.* Ecologically specialized species are likely to be more vulnerable than generalized species to changes in their environment (Jackson 1974). They may also be more likely to speciate because of their patchier distribution, and newly formed species may be more likely to persist by specializing on different resources and thus avoiding competition with other species. Certain aspects of specialization are phylogenetically conservative in at least some taxa.
2. *Geographic range.* Species with broad geographic ranges tend to have a lower risk of extinction because they are not extinguished by local environmental changes (Gaston and Blackburn 2000). They also have lower rates of speciation (Figure 7.8; Jablonski and Roy 2003), probably because they have a high capacity for dispersal and perhaps broader environmental tolerances. Geographic range size is phylogenetically conserved in molluscs, birds, and mammals; that is, there are consistent differences among clades in average range size of their component species (Jablonski 1987; Brown 1995).

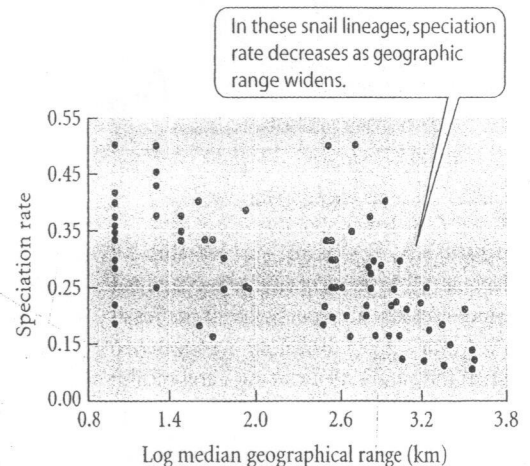


Figure 7.8 Speciation rate (expressed as the number of new species per lineage per Myr) is lower in lineages of gastropods (snails) in which the median geographical range is larger. Perhaps the average dispersal capability is greater in species of some genera than others, and this increases geographic range while lowering the rate at which geographically distant populations become different species (see Chapter 18). (After Jablonski and Roy 2003.)

3. *Population dynamics.* Species with low or fluctuating population sizes are especially susceptible to extinction. Some authors believe that speciation is also enhanced by small or fluctuating population sizes, although this hypothesis is controversial.

Do extinction rates change as clades age?

The rate of extinction of taxa in the fossil record can also be analyzed by plotting the fraction of component taxa (e.g. the fraction of genera within a family) that survive for different lengths of time (i.e., their age at extinction). This is different from asking whether or

not extinction rates have changed over the course of geological time (e.g., whether they were lower in the Jurassic than in the Devonian); instead, we ask if the rate at which members of a clade become extinct changes over the age of the clade, irrespective of when the clade originated. If the probability of extinction is independent of age, the proportion of component taxa surviving to increasingly greater ages should decline exponentially (just like the proportion of "surviving" parent atoms in radioactive decay; see Figure 4.2). Plotted logarithmically, the curve would become a straight line. If taxa become increasingly resistant to causes of extinction as they age, the logarithmic plot should be concave upward, with a long tail (Figure 7.9A).

When Leigh Van Valen (1973) plotted taxon survivorship in this way, he obtained rather straight curves, suggesting that the probability of extinction is roughly constant (Figure 7.9B). This is what we would expect if organisms are continually assaulted by new environmental changes, each carrying a risk of extinction. One possibility, Van Valen suggested, is that the environment of a taxon is continually deteriorating because of the evolution of other taxa. He proposed the **Red Queen hypothesis**, which states that, like the Red Queen in Lewis Carroll's *Through the Looking-Glass*, each species has to run (i.e., evolve) as fast as possible just to stay in the same place (i.e., survive), because its competitors, predators, and parasites also continue to evolve. There is always a roughly constant chance that it will fail to do so.

The risks of extinction do not always remain constant with age, and of course they have changed throughout the Phanerozoic. In Figure 7.10, for example, we see survivorship curves of species in various genera of Cambrian and Ordovician trilobites (Foote 1988). The Cambrian curves (Figure 7.10A) are much steeper, showing that extinction rates were higher than in the Ordovician (Figure 7.10B). Especially in the Ordovician, the curves are concave rather than straight, showing that species within a genus became extinct at a lower rate as the family aged. Perhaps species evolved greater buffering against agents of extinction. However, another possibility is that if the number of species per genus increases over time, genera will have lower extinction rates because a genus persists until all its component species have become extinct.

Causes of extinction

Extinction has been the fate of almost all the species that have ever lived, but little is known of its specific causes. Biologists agree that extinction is caused by failure to adapt to changes in the environment. Ecological studies of contemporary populations and species point to habitat destruction as the most frequent cause of extinction by far, and some cases of extinction that are due to introduced predators, diseases, and competitors have been documented (Lawton and May 1995).

When a species' environment deteriorates, some populations may become extinct, and the geographic range of the species contracts, unless formerly unsuitable sites become suitable for colonists to establish new populations. Not all environmental changes cause populations to decline, but if they do, the survival of those populations—and perhaps of the entire species—depends on adaptive genetic change. Whether or not this suffices to prevent extinction depends on how rapidly the environment (and hence the optimal phenotype)

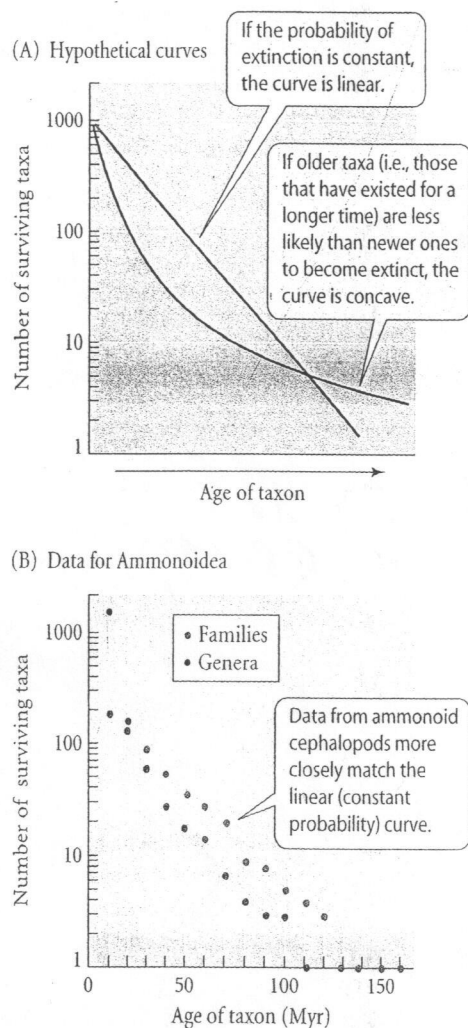


Figure 7.9 Taxonomic survivorship curves. Each curve or series of points represents the number of taxa that persisted in the fossil record for a given duration, irrespective of when they originated during geological time. (A) Hypothetical survivorship curves. In a semilogarithmic plot, the curve is linear if the probability of extinction is constant. It is concave if the probability of extinction declines as a taxon ages, as it might if adaptation lowered the long-term probability of extinction. (B) Taxonomic survivorship curves for families and genera of ammonoids. The plot for families suggests an extinction rate that is constant with age, whereas the plot for genera suggests that older survivors have a lower rate of extinction. (B after Van Valen 1973.)

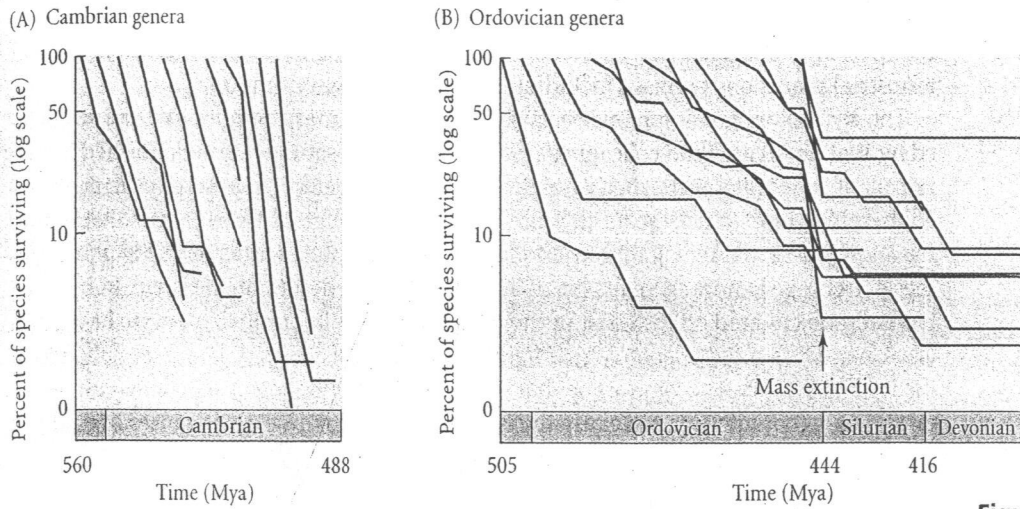


Figure 7.10 Taxonomic survivorship curves of the numbers of species in 11 Cambrian and 12 Ordovician genera of trilobites. The steeper curves in the Cambrian (A) show that extinction rates of species were greater than in the Ordovician (B). Note that the shapes of curves in (B) suggest that the extinction rate of species declined with time since the clade's origin. (After Foote 1988.)

changes relative to the rate at which a character evolves. The rate of evolution may depend on the rate at which mutation supplies genetic variation and on population size, because smaller populations experience fewer mutations. Thus an environmental change that reduces population size also reduces the chance of adapting to it (Lynch and Lande 1993). Because a change in one environmental factor, such as temperature, may bring about changes in other factors, such as the species composition of a community, the survival of a species may require evolutionary change in several or many features.

Both abiotic and biotic changes have doubtless caused extinction. For example, during the Pliocene, the rate of extinction of bivalves and many coral reef inhabitants increased, perhaps due to a decrease in temperature (Stanley 1986; Jackson and Johnson 2000). The role of competition in extinction is controversial, as we will see later in this chapter.

Mass extinctions

The history of extinction is dominated by mass extinctions at the end of the Ordovician, Devonian, Permian, Triassic, and Cretaceous periods (see Figure 7.5; Bambach 2006). The end-Permian extinction was the most drastic (Figure 7.11), eliminating about 54 percent of marine families, 84 percent of genera, and 80 to 90 percent of species (Erwin 2006). On land, major changes in plant assemblages occurred, several orders of insects became extinct, and the dominant amphibians and therapsids were replaced by new groups of therapsids (including the ancestors of mammals) and diapsids (including the ancestors of dinosaurs). The second most severe mass extinction, in terms of the proportion of taxa affected, occurred at the end of the Ordovician. Less severe, but much more famous, was

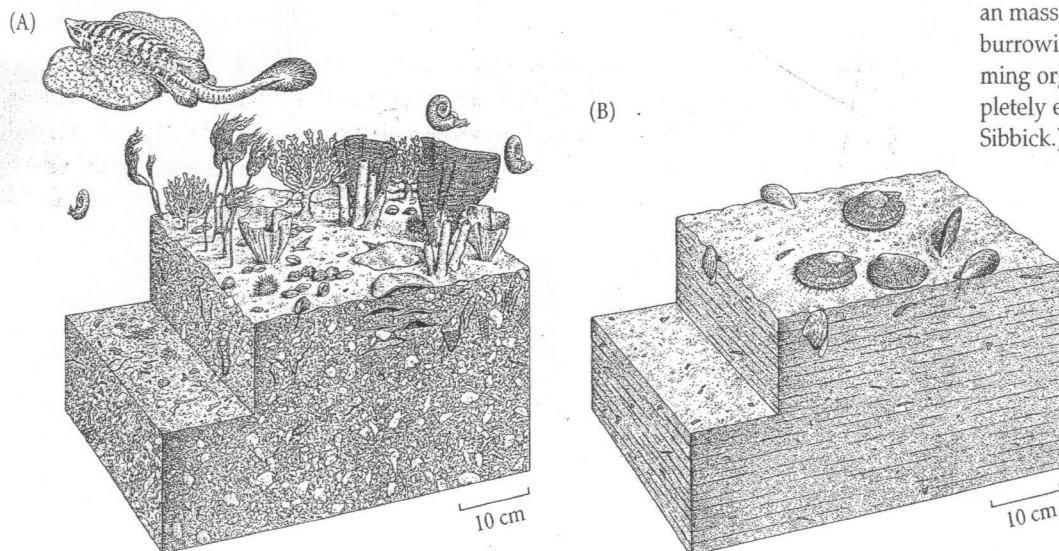


Figure 7.11 Reconstructions of an ancient seabed (A) immediately before and (B) after the end-Permian mass extinction. A rich fauna of burrowing, epifaunal, and swimming organisms was almost completely extinguished. (Artwork © J. Sibbick.)

the K/T, or end-Cretaceous, extinction, which marked the demise of many marine and terrestrial plants and animals, including the dinosaurs (except for birds).

The K/T extinction is famous because of the truly dramatic hypothesis, first suggested by Walter Alvarez and colleagues (1980), that the dinosaurs were extinguished by the impact of an extraterrestrial body—an asteroid or large meteorite. Alvarez et al. postulated that this object struck the Earth with a force great enough to throw a pall of dust into the atmosphere, darkening the sky and lowering temperatures, thus reducing photosynthesis. Geologists now agree that such an impact occurred; its site, the Chicxulub crater, has been discovered off the coast of the Yucatán Peninsula of Mexico. As we have seen (see Chapter 5), most paleontologists agree that this impact caused the mass extinction at the K/T boundary, but some argue that the impact was only one of several environmental changes that interacted to cause the K/T extinction. Likewise, the causes of the end-Permian extinction are debated, although there is increasing consensus that gases released by massive volcanic eruptions in Siberia played a dominant role.

Mass extinctions were “selective” in that some taxa were more likely than others to survive. Survival of gastropods through the end-Permian extinction was greater for species with wide geographic and ecological distributions and for genera consisting of many species (Erwin 1993). Extinction appears to have been random with respect to other characteristics, such as mode of feeding. The pattern of selectivity was much the same as during periods of background extinction, when gastropods and other taxa with broad geographic distributions had lower rates of extinction than narrowly distributed taxa (Boucot 1975). Patterns of survival through the end-Cretaceous mass extinction, however, differed from those during “normal” times (Jablonski 1995). During times of background extinction, survivorship of late-Cretaceous bivalves and gastropods was greater for taxa with planktotrophic larvae (those that feed while being dispersed by currents) and for genera consisting of numerous species, especially if those genera had broad geographic ranges. In contrast, during the end-Cretaceous mass extinction, planktotrophic and nonplanktotrophic taxa had the same extinction rates, and the survival of genera, although enhanced by broad distribution, was not influenced by their species richness. Thus the characteristics that were correlated with survival seem to have differed from those during “normal” times.

During mass extinction events, taxa with otherwise superb adaptive qualities succumbed because they happened not to have some critical feature that might have saved them from extinction under those circumstances. Evolutionary trends initiated in “normal” times were cut off at an early stage. For example, the ability to drill through bivalve shells and feed on the animals inside evolved in a Triassic gastropod lineage, but it was lost when this lineage became extinct in the late-Triassic mass extinction (Fürsich and Jablonski 1984). The same feature evolved again 120 Myr later, in a different lineage that gave rise to diverse oyster drills. A new adaptation that might have led to a major adaptive radiation in the Triassic was strangled in its cradle, so to speak.

Both physical and biotic environmental conditions were probably very different after mass extinctions than before. Perhaps for this reason, many taxa continued to dwindle long after the main extinction events (Jablonski 2002), while others, often members of previously subdominant groups, diversified. Full recovery of diversity took millions of years—as much as 100 Myr after the end-Permian disaster.

The mass extinction events, especially the end-Permian and K/T extinctions, had an enormous effect on the subsequent history of life because, to a great extent, they wiped the slate clean. Stephen Jay Gould (1985) suggested that there are “tiers” of evolutionary change, each of which must be understood in order to comprehend the full history of evolution. The first tier is microevolutionary change *within populations and species*. The second tier is “species selection,” the *differential proliferation and extinction of species* during “normal” geological times, which affects the relative diversity of lineages with different characteristics (see Chapter 11). The third tier is the *shaping of the biota by mass extinctions*, which can extinguish diverse taxa and reset the stage for new evolutionary radiations, initiating evolutionary histories that are largely decoupled from earlier ones.

Richard Bambach and colleagues (2002) found some support for Gould’s idea when they classified Phanerozoic marine animal genera by three functional criteria: whether they were

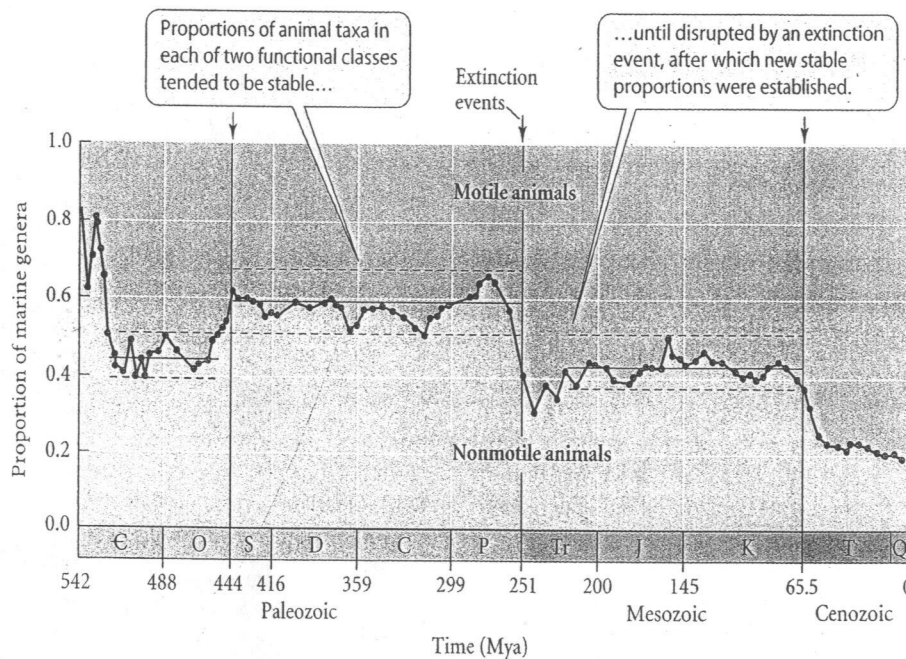


Figure 7.12 Changes in the proportions of genera of motile versus nonmotile marine animals during the Phanerozoic. The proportions were roughly stable (dashed lines) between mass extinctions, but changed abruptly to a new stable state after mass extinction events at the end of the Ordovician, Permian, and Cretaceous (black lines). Similar changes (not shown here) occurred in the proportions of predators versus nonpredators and in animals thought to be physiologically buffered versus unbuffered, based on anatomical criteria. (After Bambach et al. 2002.)

passive (nonmotile, such as barnacles) or active (motile), whether they were physiologically “buffered” (with well-developed gills and circulatory system, such as crustaceans) or not (such as echinoderms), and whether or not they were predatory. With respect to all three kinds of functional groupings, the proportions of taxa with alternative characteristics remained stable over intervals as long as 200 Myr, even though the total diversity and the taxonomic composition of the marine fauna changed greatly (Figure 7.12). However, shifts from one stable configuration to another occurred at the end of the Ordovician, Permian, and Cretaceous, suggesting that the extinction of long-prevalent (incumbent) taxa permitted the emergence of new community structures.

No truly massive extinction has occurred for 65 Myr; even the great climatic oscillations of the Pleistocene, though they altered geographic distributions and ecological assemblages, had a relatively small impact on the diversity of life. But it is depressingly safe to say that the next mass extinction has begun (Box 7A). The course of biodiversity has been altered for the foreseeable future by human domination of the Earth, and altered for the worse. Without massive, dedicated action, humanity will suffer profoundly, and much of the glorious variety of the living world will be extinguished as quickly as if another asteroid had smashed into the planet and again cast over it a pall of death.

Diversification

We turn now to the question of why increases in diversity have been greater in some lineages than in others and at some times than at others, and why diversity has tended to increase ever since the end-Permian extinction. We must ask, first, if ecosystems and the global biota tend to reach an equilibrium number of species, and second, what might change such an equilibrium.

Modeling rates of change in diversity

The number of taxa (N) changes over time by origination (as a result of branching of lineages) and extinction. These events are analogous to the births and deaths of individual organisms in a population, so models of population growth can be adapted to describe changes in taxonomic diversity. For each time interval Δt , suppose S new taxa originate per taxon present at the start of the interval, and suppose E is the number of taxa that become extinct, per original taxon, during the interval. Then ΔN , the change in N , equals

BOX 7A The Current Mass Extinction

For the first time in the history of life, a single species has precipitated a mass extinction. Within the next few centuries, the diversity of life will almost certainly plummet at a greater pace than ever before.

The human threat to Earth's biodiversity has accelerated steadily with the advent of ever more powerful technology and the exponential growth of the world's human population, which is approaching 7 billion as of mid-2009. The per capita rate of population growth is greatest in the developing countries, which are chiefly tropical and subtropical, but the per capita impact on the world's environment is greatest in the most highly industrialized countries. An average American, for example, has perhaps 140 times the environmental impact of an average Kenyan, because the United States is so profligate a consumer of resources harvested throughout the world, and of energy (with impacts ranging from strip mines and oil spills to insecticides and production of the "green-

house gases" that cause global warming).

Some species are threatened by hunting or overfishing, and others by species that humans have introduced into new regions. But by far the greatest cause of extinction, now and probably over the course of the twenty-first century, is the destruction of habitat (Sala et al. 2000). It is largely for this reason that 29 percent of North American freshwater fishes are endangered or already extinct, and that about 10 percent of the world's bird species are considered endangered by the International Council for Bird Preservation.

The numbers of species likely to be lost are highest in tropical forests, which are being destroyed at a phenomenal and accelerating rate. As E. O. Wilson (1992) said, "in 1989 the surviving rain forests occupied an area about that of the contiguous forty-eight states of the United States, and they were being reduced by an amount equivalent to the size of Florida each year." Several authors have estimated that 10 to 25 per-

cent of tropical rain forest species—accounting for as much as 5 to 10 percent of Earth's species diversity—will become extinct in the next 30 years. To this toll must be added extinctions caused by the destruction of species-rich coral reefs, pollution of other marine habitats, and losses of habitat in areas such as Madagascar and the Cape Province of South Africa, that harbor unusually high numbers of endemic species.

In the long run, an even greater threat to biodiversity may be global warming caused by high and increasing consumption of fossil fuels and production of carbon dioxide and other "greenhouse" gases. Earth's climate has warmed by a global average of 0.6°C during the last century, and the rate of warming is accelerating. Although climate change will vary in different regions (some will actually suffer a cooling trend), snow cover, glaciers, and polar ice caps are rapidly shrinking, and some tropical areas are becoming much drier. These changes are happening

the number of "births," SN , minus the number of "deaths," EN , and the rate of change in diversity (the **diversification rate**), $\Delta N/\Delta t$, is

$$\frac{\Delta N}{\Delta t} = SN - EN \quad \text{or} \quad \frac{\Delta N}{\Delta t} = RN$$

where $R = (S - E)$ and is the **PER CAPITA RATE OF INCREASE**. The growth in number of taxa is positive if $R > 1$.

Between the beginning (time t_0) and end (time t_1) of the time interval, the "population" grows by multiplying its original size by the per capita rate of increase: $N_1 = N_0R$. If the rates S and E remain constant, then after the next interval Δt , the population will be $N_2 = N_1R = N_0R^2$. In general, after t time intervals, the number of taxa will be

$$N_t = N_0R^t$$

as long as the per capita origination and extinction rates remain the same. This equation describes **exponential growth** of the number of taxa (or of a population of organisms) (Figure 7.13A). For continuous growth, rather than growth in discrete intervals, the equivalent expressions are

$$\frac{dN}{dt} = rN \quad \text{and} \quad N_t = N_0e^{rt}$$

where r is the **INSTANTANEOUS PER CAPITA RATE OF INCREASE**.

Let us pursue the analogy between the number of taxa and the number of organisms in a population (in which, as we know, birth and death rates are not constant). Factors such as severe weather may alter these rates by proportions that are unrelated to the density of the population. In contrast, **density-dependent factors**, which include competition

BOX 7A (Continued)

much faster than most of the climate changes that have occurred in the past. Some species may adapt by genetic change, but there is already evidence that many species will shift their ranges. Such shifts, however, are difficult or impossible for most mountaintop and Arctic species, and for many others because their habitats and the habitat "corridors" along which they might disperse have been destroyed. Computer simulations, based on various scenarios of warming rate and species' capacity for dispersal, suggest that within the next 50 years, between 18 and 35 percent of species will become "committed to extinction"—that is, they will have passed the point of no return (Thomas et al. 2004).

If mass extinctions have happened naturally in the past, why should we be so concerned? Different people have different answers, ranging from utilitarian to aesthetic to spiritual. Some point to the many thousands of species that are used by humans today, ranging from familiar foods to fiber, herbal medicines,

and spices used by peoples throughout the world. Others cite the economic value of ecotourism and the enormous popularity of bird-watching in some countries. Biologists will argue that thousands of species may prove useful (as many already have) as pest-control agents, or as sources of medicinal compounds or industrially valuable materials. Except in a few well-known groups, such as vertebrates and vascular plants, most species have not even been described, much less been studied for their ecological and possible social value.

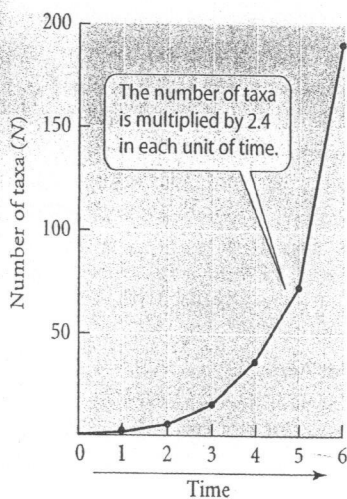
The rationale for conserving biodiversity is only partly utilitarian, however. Many people (including this author) cannot bear to think that future generations will be deprived of tigers, sea turtles, and macaws. They share with millions of others a deep renewal of spirit in the presence of unspoiled nature. Still others feel that it is in some sense cosmically unjust to extinguish, forever, the species with which we share the Earth.

Conservation is an exceedingly com-

plicated topic; it requires not only a concern for other species, but compassion and understanding of the very real needs of people whose lives depend on clearing forests and making other uses of the environment. It requires that we understand not only biology, but also global and local economics, politics, and social issues ranging from the status of women to the reactions of the world's peoples and their governments to what may seem like elitist Western ideas. Anyone who undertakes work in conservation must deal with these complexities. But everyone can play a helpful role, however small. We can try to waste less; influence people about the need to reduce population growth (surely the most pressing problem of all); support conservation organizations; patronize environment-conscious businesses; stay aware of current environmental issues; and communicate our concerns to elected officials at every level of government. Few actions of an enlightened citizen of the world can be more important.

for food or space, cause the per capita birth rate to decline, and/or the death rate to increase, with population density, so that population growth slows down and the population density may reach a stable equilibrium (Figure 7.13B). Paleobiologists have suggested that changes in the number of species or higher taxa may similarly be affected by **diversity-dependent factors** that might reduce origination rates or increase extinction rates as the number of species increases. For example, competition among species for resources might limit the possible number of species to some maximal number, say K .

(A) Discontinuous exponential growth



(B) Continuous exponential and logistic growth

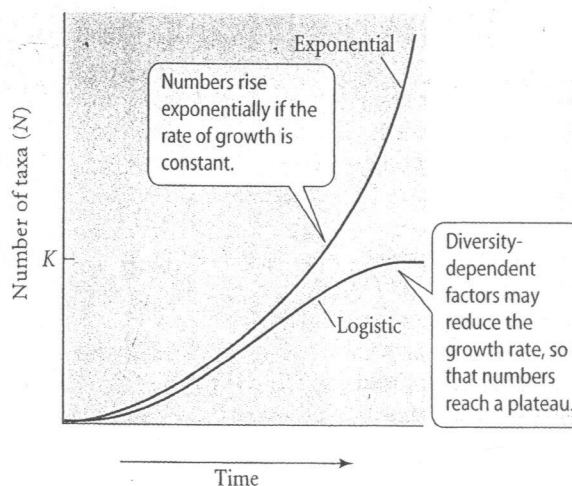


Figure 7.13 (A) Theoretical increase in the number of taxa (N), according to the equation $N_t = N_0 R^t$, where R is the rate of increase in each discrete time interval (in this example, $R = 2.4$). (B) The increase in the number of taxa when change is continuous. The number of taxa grows exponentially if the rate of increase (r) is constant, but levels off if growth is logistic (i.e., if the rate of increase is negatively diversity-dependent).

Ecologists describe density-dependent population growth by the LOGISTIC EQUATION, which for growth in numbers of species may be expressed as

$$\frac{\Delta N}{\Delta t} = r_0 N \left(\frac{K - N}{K} \right)$$

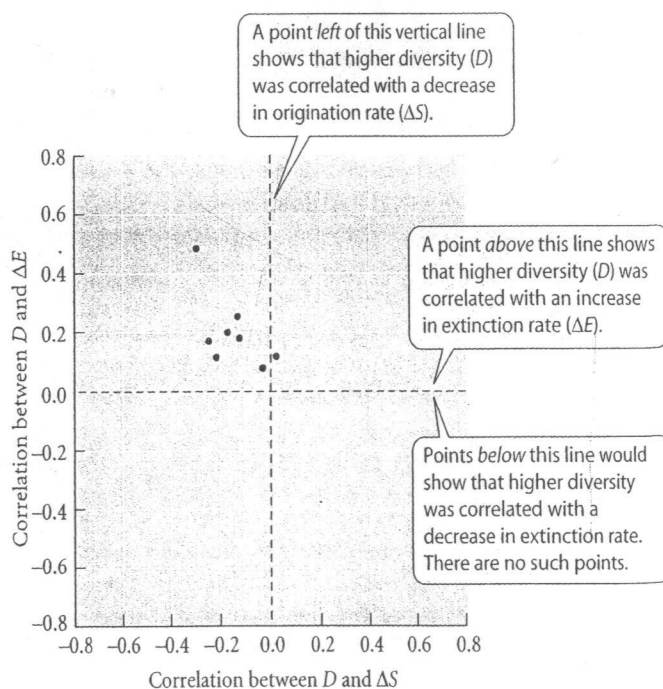
where R_0 is the per capita rate of increase when the number of species is very low. Then the increase in number, $\Delta N/\Delta t$, declines as N increases and $(K - N)$ goes toward zero. At equilibrium, when $\Delta N/\Delta t = 0$, $N = K$.

Does species diversity reach equilibrium?

A huge ecological literature is concerned with whether or not the number of coexisting species (of some group such as plants or mammals) tends toward an equilibrium. This question is complex and not entirely resolved, but ecologists agree that some factors tend to limit species diversity. The space that plants compete for and the energy flux that organisms depend on are finite, so they can be divided among a limited number of species populations that are still large enough to persist. Moreover, phenomena such as competitive exclusion of species from each others' ranges (e.g., Figure 6.20) show that interactions among species can tend to limit local species diversity.

The fossil record supports the hypothesis that the per capita rate of increase in the number of species (or higher taxa) is lowered as the number grows. For example, Michael Foote (2000b), using Sepkoski's database, calculated changes (ΔS or ΔE) in the per capita rate of origination (S) or extinction (E) of genera from one stratigraphic stage to the next, and correlated these short-term changes with the number of genera present (D) at the beginning of the interval (Figure 7.14). For each of several phyla, correlations between ΔS and D were negative: the higher diversity is at the beginning of a time interval, the lower the rate of origination of new genera. Conversely, correlations between ΔE and D were positive: the higher diversity is, the higher the proportion of genera that become extinct. Whereas Foote found evidence of diversity-dependence in both origination and extinction rates, Alroy (1998) found that rates of origination of genera and species of mammals were diversity-dependent, but extinction rates were apparently not. Both these and other studies imply that the diversity of taxa should tend toward a stable equilibrium. Why, then, has diversity not remained constant?

Figure 7.14 The correlation between diversity (D) in a geological stage and changes in origination (ΔS) and extinction (ΔE) rates from the mid-Jurassic to the Cenozoic. A point above the horizontal 0.0 line indicates a positive correlation (>0) between diversity and the per capita rate of extinction, as expected if higher diversity increases extinction risk. A point left of the vertical 0.0 line shows a negative correlation (<0) between diversity and per capita origination rate, suggesting that origination of new taxa is inhibited by greater standing diversity. The graph shows that high diversity was associated with an increase in the extinction rate and a decrease in the origination rate—evidence of diversity-dependent damping of growth in diversity. (After Foote 2000b.)



A system may shift from one equilibrium state to another when conditions change. At least three kinds of changes have altered conditions for organisms. First, changes have occurred in the physical environment, including changes in climate and in the configuration of land and sea. Second, the taxa that became dominant after mass extinctions were different from those that prevailed before, and would be expected to attain a different equilibrium level of diversity because of new patterns of competition and other interactions. There is no reason, for example, to expect the diversity of large herbivores and carnivores to be the same when they are mammals as when they are dinosaurs. Third, taxa have evolved to use new resources and habitats, changing the overall number of species that the planet's resources can support.

RELEASE FROM COMPETITION. Studies of both living and extinct organisms have shown that lineages often have diversified most rapidly when presented with ecological opportunity: what is often called "ecological space" or "vacant niches" not occupied by other species. In many isolated islands and bodies of water, descendants of just a few original colonizing species have diversified and filled ecological niches that are occupied in other places by unrelated organisms. Such adaptive radiations include the cichlid fishes in the Great Lakes of eastern Africa, the honeycreepers in the Hawaiian Islands, and Darwin's finches in the Galápagos Islands (see Figure 3.23). Islands and other habitats with taxonomically depauperate biotas typically harbor organisms that have evolved unusual new ways of life. For example, the larvae of almost all moths and butterflies are herbivorous, but in the Hawaiian Islands, the larvae of the moth genus *Eupithecia* are specialized for predation (Figure 7.15; Montgomery 1982). Probably such unusual forms are more prevalent where species diversity is reduced because they are not faced with as many predators or superior competitors in their early, relatively inefficient, stages of adaptation to new ways of life.

The fossil record provides many instances in which the reduction or extinction of one group of organisms has been followed or accompanied by the proliferation of an ecologically similar group. For example, conifers and other gymnosperms declined as angiosperms (flowering plants) diversified, and the orders of placental mammals appear in the fossil record after the late Cretaceous extinction of the nonavian dinosaurs.

Several hypotheses can account for these patterns (Benton 1996; Sepkoski 1996a). Two of these hypotheses involve competition between species in two clades. On one hand, the later group may have *caused* the extinction of the earlier group by competition, a process called **competitive displacement** (Figure 7.16A). On the other hand, an incumbent taxon may have *prevented* an ecologically similar taxon from diversifying, because it already "occupies" resources. Extinction of the incumbent taxon may then have vacated ecological "niche space," permitting the second taxon to radiate (Figure 7.16B). This process has been called **incumbent replacement** by Rosenzweig and McCord (1991), who argued that

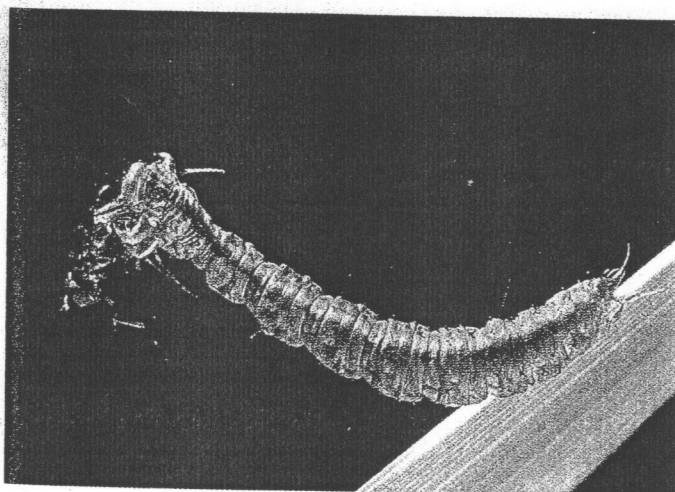
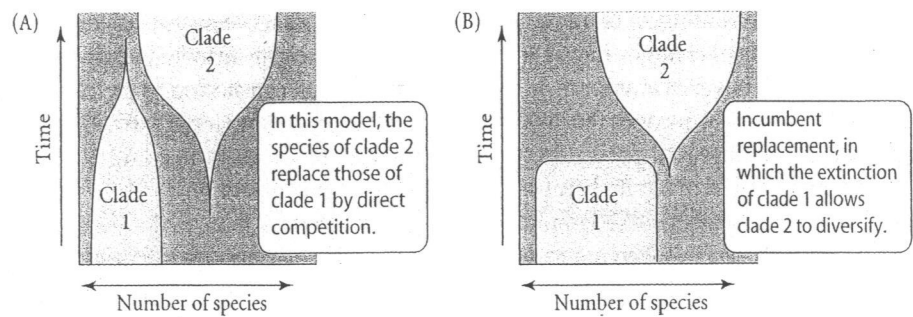


Figure 7.15 A predatory moth caterpillar (*Eupithecia*) in the Hawaiian Islands, holding a *Drosophila* that it has captured with its unusually long legs. Predatory behavior is extremely unusual in the order Lepidoptera. (Photo by W. P. Mull, courtesy of W. P. Mull and S.L. Montgomery.)

Figure 7.16 Models of competitive displacement and replacement. In each diagram, the width of a “spindle” represents the number of species. (A) Competitive displacement, in which the increasing diversity of clade 2 causes a decline in clade 1 by direct competitive exclusion. (B) Incumbent replacement, in which the extinction of clade 1 enables clade 2 to diversify. (After Sepkoski 1996a.)



the second taxon may have had superior adaptive features, but nevertheless could not have displaced the earlier taxon by competition.

There are good reasons to believe that competition among species has affected changes in diversity (Sepkoski 1996a). The rate of origination of new taxa has been much greater at times when diversity was unusually low—namely, during the Cambrian and after mass extinction events—than at other times (see Figure 7.4A). But how competition has affected changes in diversity is controversial.

Sepkoski et al. (2000) developed a mathematical model in which two clades increase in diversity following the logistic equation, but in which the increase in each clade is inhibited by both its own diversity and that of the other. They applied the model to data on the number of genera of two groups of bryozoans (“moss animals”), the cyclostomes and the cheilostomes. When these two groups meet, cheilostomes generally overgrow cyclostomes (Figure 7.17A). Especially after the end-Permian extinction, the diversity of cheilostomes has increased, whereas cyclostomes have not recovered (Figure 7.17B). When Sepkoski et

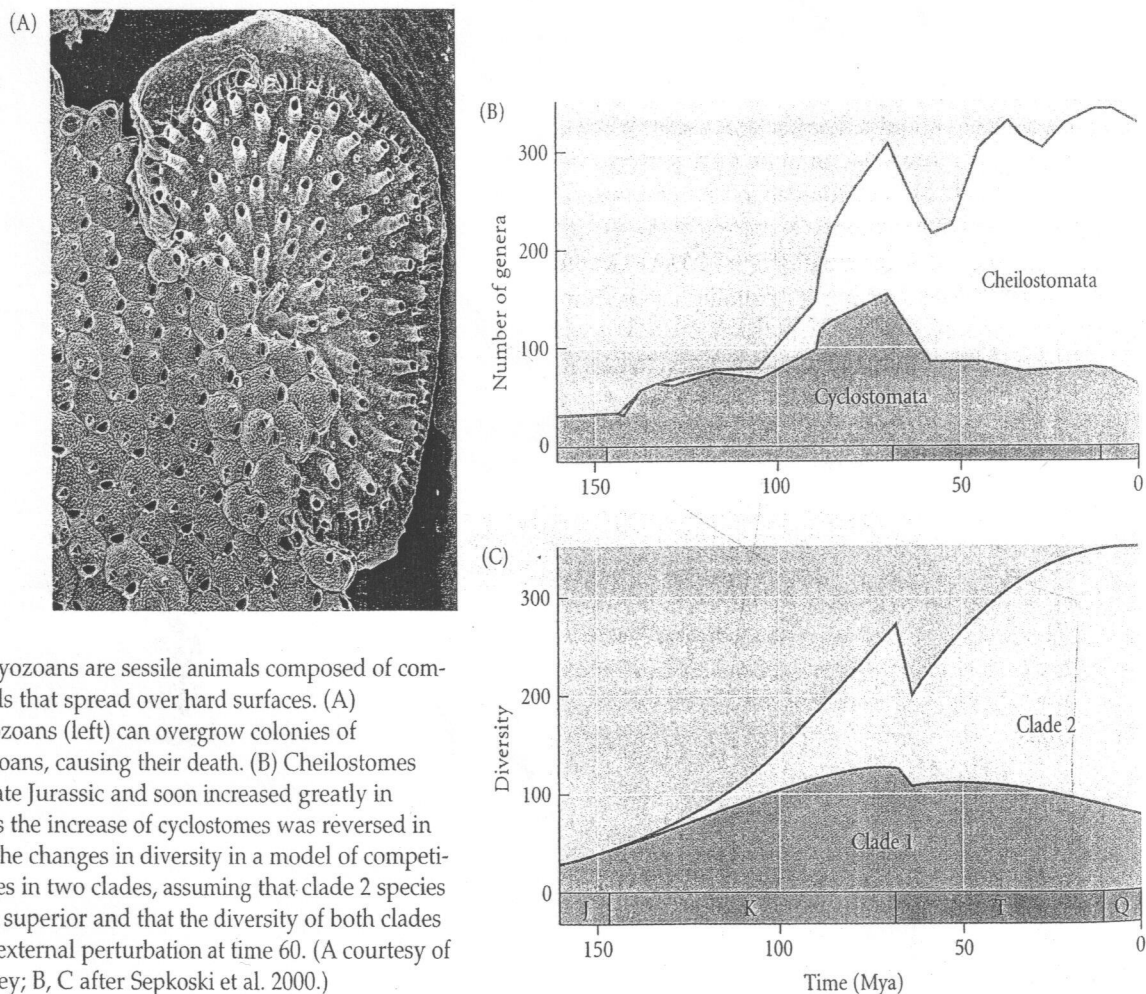


Figure 7.17 Bryozoans are sessile animals composed of component individuals that spread over hard surfaces. (A) Cheilostome bryozoans (left) can overgrow colonies of cyclostome bryozoans, causing their death. (B) Cheilostomes appeared in the late Jurassic and soon increased greatly in diversity, whereas the increase of cyclostomes was reversed in the Tertiary. (C) The changes in diversity in a model of competition among species in two clades, assuming that clade 2 species are competitively superior and that the diversity of both clades is reduced by an external perturbation at time 60. (A courtesy of Frank K. McKinney; B, C after Sepkoski et al. 2000.)

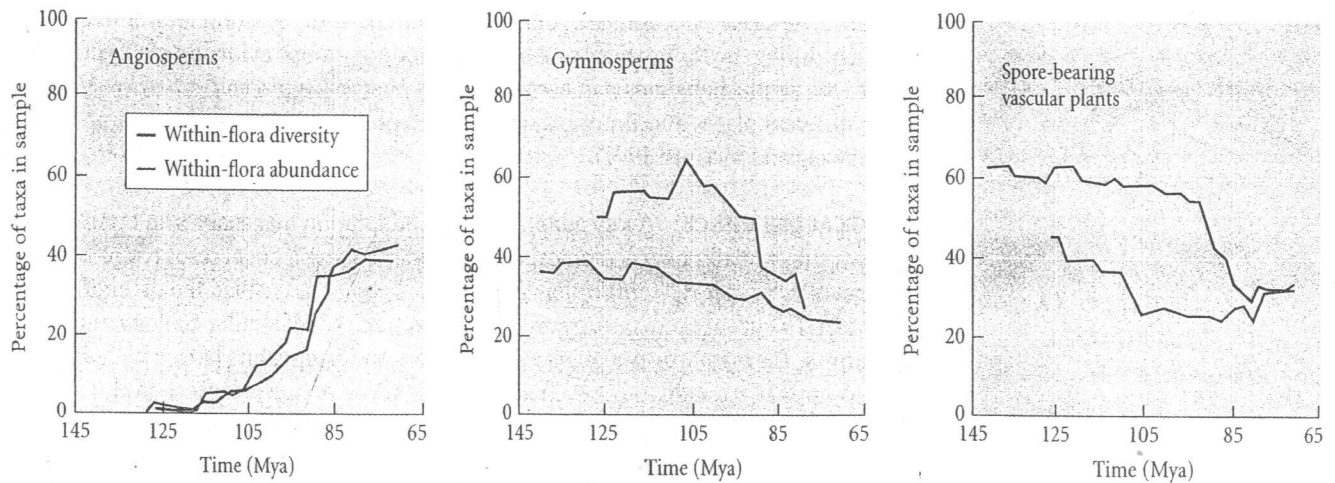


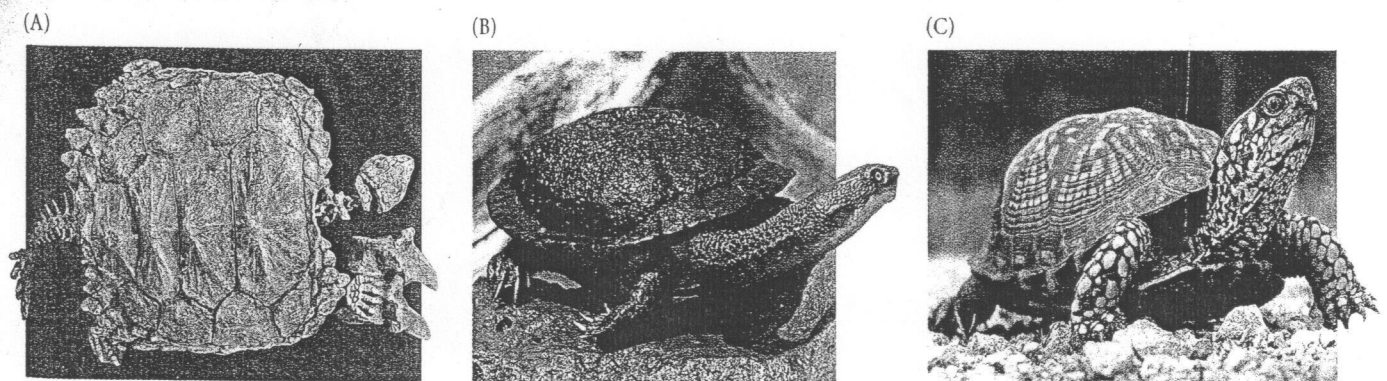
Figure 7.18 Changes in relative diversity (blue curves) and abundance (red curves) of major groups of vascular plants in fossil samples during the Cretaceous. The increase in both diversity and abundance of flowering plants was mirrored by the decline, in both respects, of the spore-bearing plants (e.g., ferns) and the decline in abundance of gymnosperms (e.g., conifers). This pattern is consistent with competitive displacement. (After Lupia et al. 1999.)

al. simulated the Permian drop in the diversity of both clades, their model rendered a profile of diversity change that closely matches the data (Figure 7.17C). This result does not prove that competition determined the history of bryozoan diversity, but it is consistent with that hypothesis.

A pattern of replacement is consistent with competitive displacement if the earlier and later taxa lived in the same place at the same time, if they used the same resources, if the earlier taxon was not decimated by a mass extinction event, and if the diversity and abundance of the later taxon increased as the earlier one declined (Lupia et al. 1999). Vascular plants, which certainly compete for space and light, showed this pattern during the Cretaceous, when flowering plants increased in diversity and abundance at the expense of nonflowering plants, especially spore-bearing plants such as ferns (Figure 7.18).

Incumbent replacement has probably been more common than competitive displacement (Benton 1996). The great radiation of placental mammals in the early Cenozoic is often credited to the K/T extinction of the last nonavian dinosaurs and other large “reptiles,” which may have suppressed mammals by both competition and predation. This is one of many examples of a long delay between the origin of a clade and its diversification and rise to ecological prominence, a delay that may often be caused by incumbent suppression of the new clade (Jablonski 2008). The best evidence of incumbency and release is supplied by repeated replacements. For instance, amphichelydians, the “stem group” of turtles, could not retract their heads and necks into their shells (Figure 7.19). Two

Figure 7.19 Pleurodiran and cryptodiran turtles replaced incumbent amphichelydian turtles, which became entirely extinct. (A) Amphichelydians, represented by the reconstructed skeleton of the earliest known turtle (*Proganochelys quenstedti*, upper Triassic), could not retract their heads for protection. (B) Snakeneck turtles such as *Chelodina longicollis* are pleurodiran turtles that flex the neck sideways beneath the edge of the carapace. (C) Cryptodiran turtles, represented here by an Eastern box turtle (*Terrapene carolina*), fully retract the head into the shell by flexing the neck vertically. (A courtesy of E. Gaffney, American Museum of Natural History; B © Juniors Bildarchiv / Alamy; C © Constance McGuire / istockphoto.com.)



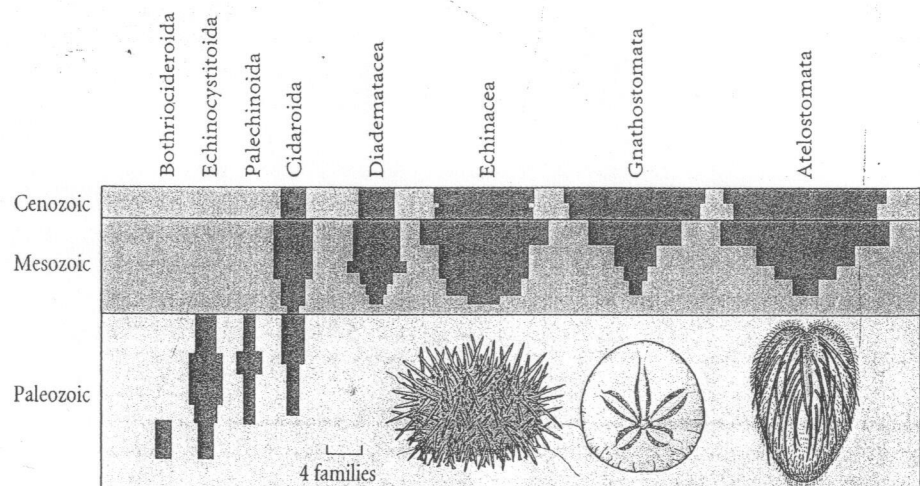
groups of modern turtles, which protect themselves by bending the neck under or within the shell, replaced the amphichelydians in different parts of the world four or five times, especially during the K/T extinction event. The modern groups evidently could not radiate until the amphichelydians had become extinct. That this replacement occurred in parallel in different places and times makes it a likely example of release from competition (Rosenzweig and McCord 1991).

ECOLOGICAL DIVERGENCE. A **key adaptation** is an adaptation that enables an organism to occupy a substantially new ecological niche, often by using a novel resource or habitat. The term often carries the implication that the adaptation has enabled the diversification of a group. The group may occupy an **adaptive zone**, a set of similar ecological niches. For example, the many species of insectivorous bats and fruit-eating bats, which are nocturnal, occupy two adaptive zones that differ from those of diurnal insect- and fruit-eating birds. The term **ecological space** is roughly equivalent to a set of adaptive zones.

The evolution of the ability to use new resources or habitats has certainly contributed importantly to the increase in diversity over time (Niklas et al. 1983; Bambach 1985). Among the sea urchins (Echinoidea), for example, three orders increased greatly in diversity beginning in the early Mesozoic (Figure 7.20). The order Echinacea evolved stronger jaws that enabled them to use a greater variety of foods, while the heart urchins (Atelostomata) and sand dollars (Gnathostomata) became specialized for burrowing in sand, where they feed on fine particles of organic sediment. The key adaptations allowing this major shift of habitat and diet include a flattened form and a variety of highly modified tube feet that can capture fine particles and transfer them to the mouth. Much of the history of increase in marine animal diversity throughout the Phanerozoic can be explained by increases in the occupancy of ecological space accomplished by evolutionary innovations such as those of the sand dollars (Bambach 1985; see Figure 7.12). Expansion into new habitats and feeding habits accounts for the diversification of most families of tetrapod vertebrates, such as various groups of frogs, snakes, and birds (Benton 1996).

Although, as in the sand dollars, the diversification of a clade can often be plausibly ascribed to a key adaptation, this is extremely difficult to demonstrate from a single case because the diversity might be due to other causes. Stronger evidence is provided if the rate of diversification is consistently associated with a particular kind of character that has evolved independently in a number of different clades. Such tests have been applied mostly to living organisms. The diversity of a number of clades with a novel character can be compared with the diversity of their sister groups that retain the ancestral character state. Since sister taxa are equally old, the difference between them in number of species must be due to a difference in rate of diversification, not to age. If the convergently evolved character is consistently associated with high diversity, we would have support for the hypothesis that it has caused a higher rate of diversification.

Figure 7.20 Changes in the diversity of several groups of echinoid echinoderms during the Mesozoic and Cenozoic. Diversification of sea urchins (order Echinacea), sand dollars (Gnathostomata), and heart urchins (Atelostomata) greatly increased, probably because of key adaptations described in the text. The width of the symmetrical profile of each group represents the number of families in that group at successive times. (After Bambach 1985.)



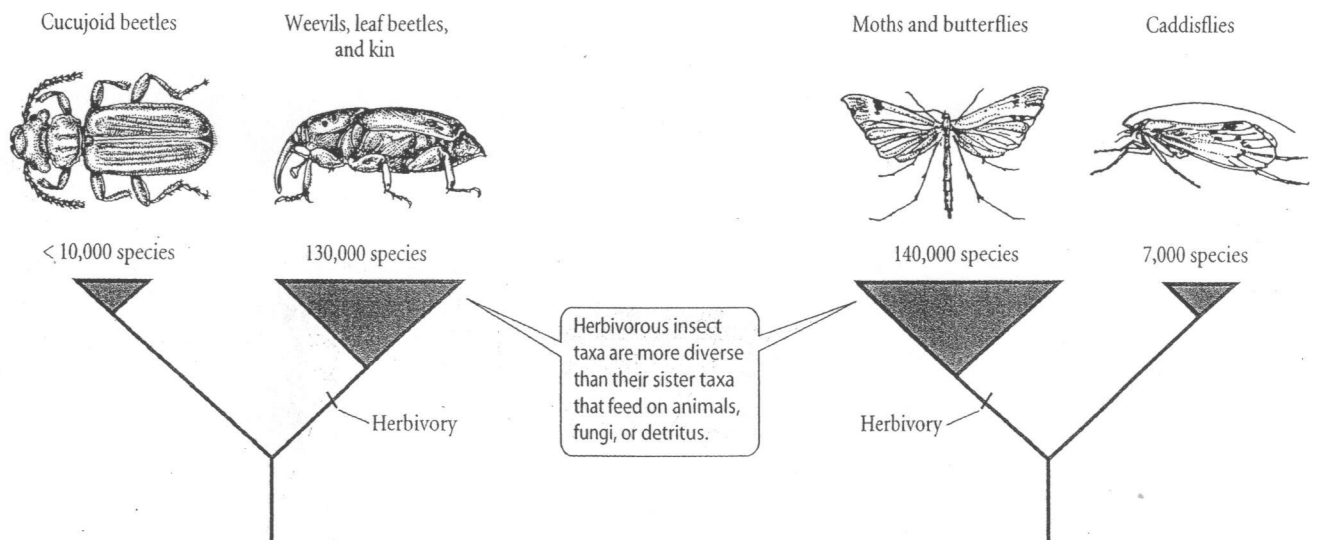


Figure 7.21 Two replicated sister-group comparisons of herbivorous clades of insects with their sister clades that feed on animals, fungi, or detritus. Herbivorous clades are consistently more diverse, demonstrating higher rates of diversification. (Data from Mitter et al. 1988.)

Charles Mitter and colleagues (Mitter et al. 1988; Farrell et al. 1991) applied this method, called **REPLICATED SISTER-GROUP COMPARISON**, to herbivorous insects and plants. The habit of feeding on the vegetative tissues of green plants has evolved at least 50 times in insects, usually from predatory or detritus-feeding ancestors. Phylogenetic studies have identified the nonherbivorous sister group of 13 herbivorous clades. In 11 of these cases, the herbivorous lineage has more species than its sister group (Figure 7.21). This significant correlation supports the hypothesis that entry into the herbivorous adaptive zone has promoted diversification. These researchers then examined the species diversity of 16 clades of plants that have evolved rubbery latex (as in milkweeds) or resin (as in pines), both of which deter attack by herbivorous insects. Thirteen of these clades have more species than their sister clades, which lack latex or resin. These defensive features may have fostered diversification.

From studies of modern organisms, we know that much diversity resides in the great numbers of related species that reduce competition with one another by subtle differences in resource use. Anoles living together on an island, for example, forage in different microhabitats (see Figure 6.23). Some paleontologists have suggested that subdivision of niches has increased over time because individual fossil deposits, which generally record local communities, contain more species in later than in earlier geological periods (Benton 1990). The increase in species number seems greater than the increase in the variety of major growth forms or adaptive zones, suggesting that the ever greater number of species coexisted by more finely partitioning similar resources.

PROVINCIALITY. The degree to which the world's biota is partitioned among geographic regions is called **provinciality**. A faunal or floral province is a region containing high numbers of distinctive, localized taxa (see Chapter 6). The fauna and flora of the contemporary world are divided into more provinces than ever before in the history of life. A trend from a cosmopolitan distribution of taxa to more localized distributions has persisted throughout much of the Mesozoic and Cenozoic and is thought by many paleontologists to be one of the most important causes of the increase in global diversity during this time (Valentine et al. 1978; Signor 1990).

Among marine animals, the number of faunal provinces was relatively low throughout much of the Paleozoic, and it dropped to an all-time low in the early Triassic, when most of the higher taxa that had survived the end-Permian mass extinction were so highly cosmopolitan that paleontologists recognize only a single, worldwide province during that time. During the Jurassic and Cretaceous, and especially the Tertiary, marine animals were distributed among an increasing number of latitudinally arranged provinces in both the Atlantic and Pacific regions. Similarly, among terrestrial vertebrates, a distinct fauna developed on each major land mass during the later Mesozoic and the Cenozoic, and the

broad latitudinal distributions of many dinosaurs and other Mesozoic groups gave way to the much narrower latitudinal ranges of today's vertebrates.

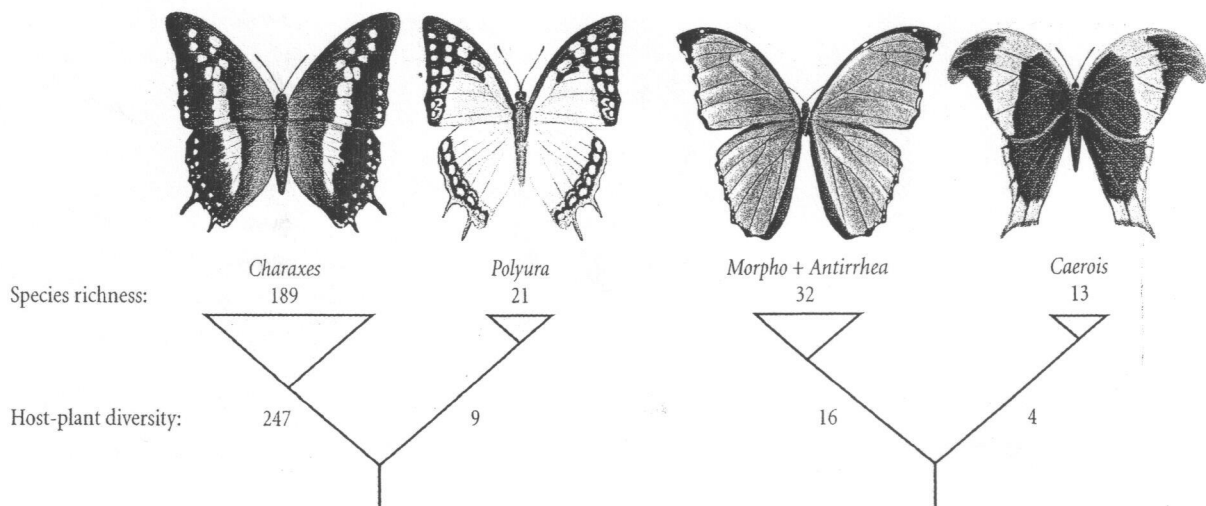
Changes in the distribution of land masses as a result of plate tectonic processes are the fundamental cause of this trend. After the breakup of Pangaea in the Triassic, land masses ultimately became arrayed almost from pole to pole along a wider latitudinal span than ever before in Earth's history. This deployment of the continents created two increasingly disjunct ocean systems, the Indian-Pacific and the Atlantic, and established a pattern of ocean circulation that created a stronger latitudinal temperature gradient than ever before (Valentine et al. 1978). Not only did the variety of environments increase, but the fragmentation of land masses also allowed for divergent evolution and prevented the interchange of species that, by competition or predation, might lower diversity.

OTHER INFLUENCES ON DIVERSIFICATION. Interactions among species affect changes in diversity in many and complex ways that have not been fully analyzed. As we have seen, the diversification of one clade may suppress the diversification of competing organisms, or even reduce their diversity. Predators that have been introduced by humans into new regions have extinguished many species, but whether or not increases in the diversity of predators have affected the diversity of prey species on evolutionary time scales is uncertain. The Phanerozoic trends toward increased frequency of predatory marine animals and nonpredatory mobile and infaunal animals seem to be statistically independent; there is no evidence that one caused the other (Madin et al. 2006).

However, an increase in the number of species in a clade almost surely results, sooner or later, in an increase of affiliated species—especially parasites and mutualists—that use them as resources. The evidence that diversity thereby begets more diversity comes largely from studies of living organisms. For example, tropical forests contain far more species of herbivorous insects than temperate forests do, because tropical forests have more species of plants—resources on which the insects are specialized to some extent. The studies that have documented this pattern differ on whether or not the tropical insects are more specialized, more host-specific, than insects in temperate forests (Novotny et al. 2006, 2007; Dyer et al. 2007). Using a phylogeny of the largest family of butterflies, Niklas Janz and colleagues (2006) chose pairs of sister taxa that differ in the diversity of plants that their larvae eat. In 18 of 22 such pairs, the group with the higher diversity of host plants has the higher number of species, as expected if the diversification of plants has contributed to speciation and diversification of the insects (Figure 7.22). In many such cases, a molecular clock analysis has shown that the insects have diversified after the divergence among the plant lineages that they now use (Winkler and Mitter 2008).

Major changes in climate have been associated with increases in extinction and with changes in the distribution of habitats and vegetation types, which in turn have facilitat-

Figure 7.22 Examples of pairs of sister groups of nymphalid butterflies that differ in species richness (indicated at the branch tips). The more species-rich groups feed on a greater variety of larval host-plants, as indicated along the branches. Adaptation to a greater variety of food resources may have enhanced diversification. (Data from Janz et al. 2006.)



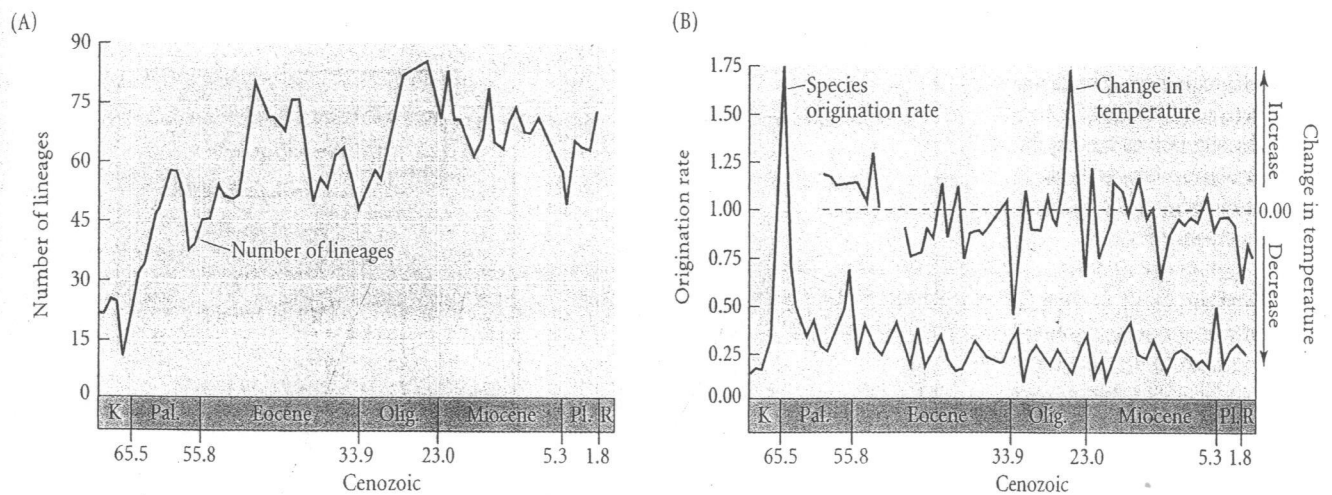


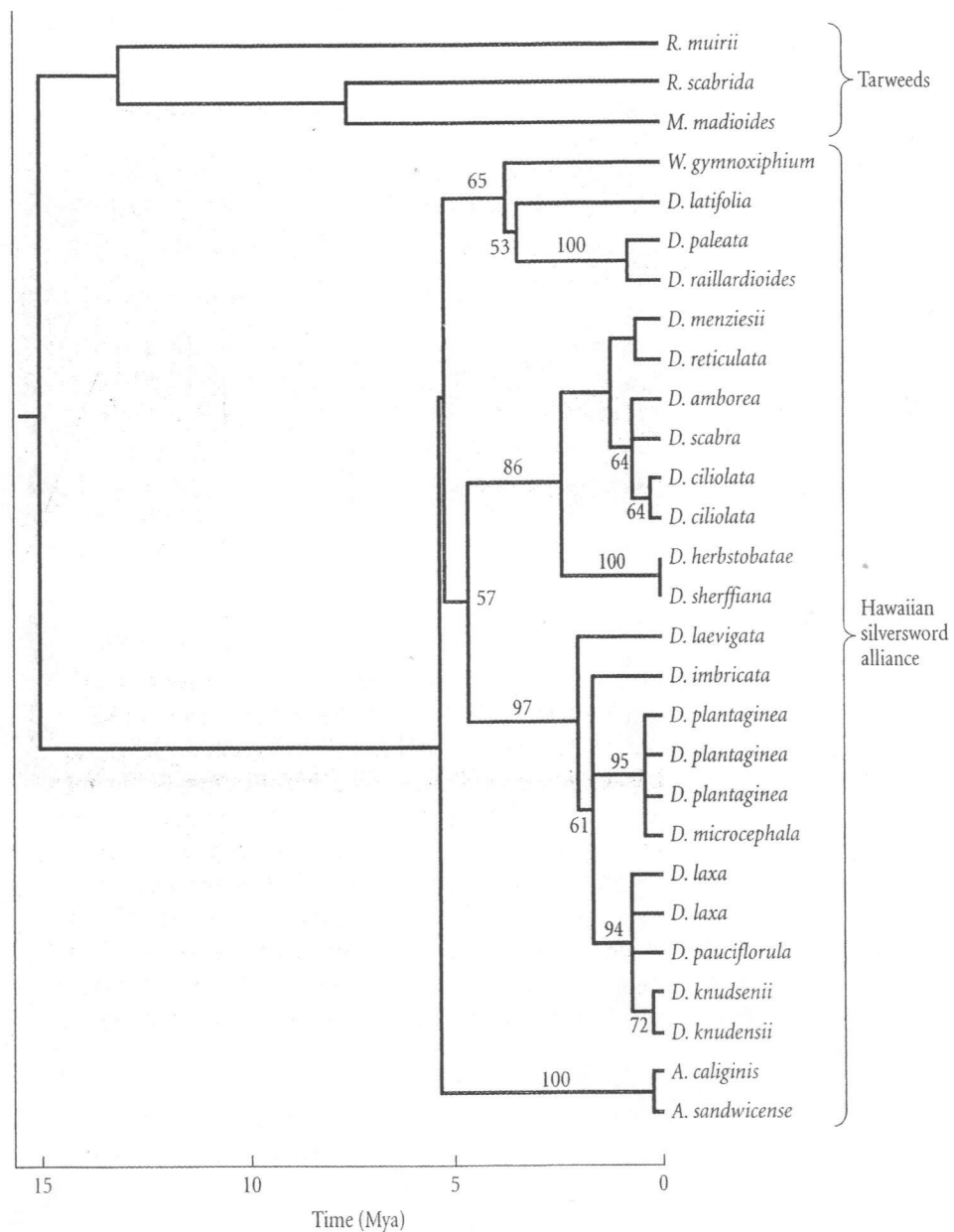
Figure 7.23 Changes in taxonomic diversity of Cenozoic mammals in North America. (A) The estimated history of diversity. (B) Fluctuations in the rate of origination of new lineages (black curve), compared with concurrent changes in temperature (red curve). The changes in temperature seem unrelated to origination rate, although some of them match declines in diversity that are evident in (A). (After Alroy et al. 2000.)

ed major changes in the distributions of taxa, often leading to diversification (Rothschild and Lister 2003). Thus, it is not known exactly how climate changes may have affected rates of origination and extinction; they may have had direct effects, but it is more likely that they have influenced diversification indirectly, through biotic changes. For example, in the mid-Eocene, about 50 to 40 Mya, the climate became cooler and drier, subtropical forests were widely replaced by savannahs in much of the temperate zone, and the diversity of primates and other arboreal mammals declined while that of large herbivores increased (Janis 1993). On the whole, however, changes in the rates of origination and extinction of mammals during the Tertiary are not closely correlated with changes in temperature (Figure 7.23). The importance of climate change in the evolution of diversity, relative to other factors such as key innovations and biotic interactions, is not yet well known (Alroy et al. 2000).

PHYLOGENETIC ANALYSES OF DIVERSITY TRENDS. It is possible to make inferences about the rate of increase in the number of species in a clade from a molecular phylogeny of living species, if the data are consistent with a molecular clock (Nee 2006). For example, Figure 7.24 is a phylogeny of the Hawaiian silverswords (see Figure 3.24), the diversification of which began at most 15 Mya (Baldwin and Sanderson 1998). The number of lineages increases from 1 (the common ancestor at 15 Mya) to 28 extant species. Now recall that if the rate of increase (r) in the number of lineages (N) has been constant, the number of lineages grows exponentially as $N_t = N_0 e^{rt}$. Taking the natural logarithm (\ln) of both sides of the equation, $\ln(N_t) = \ln(N_0) + rt$. That is, the log of the number of lineages increases linearly, with slope r . Slope r is the difference between the per capita rates of origination or speciation (S) and extinction (E), so the slope estimates the speciation rate if we assume there has been no extinction. If there have been species extinctions, however, the slope of the plot equals $S - E$ in the relatively distant past. But unless the extinction rate is high, species that arose recently have not yet had time to become extinct, so the slope must be closer to S in the very recent past (Figure 7.25A). Thus, it is possible to estimate both the speciation rate and the extinction rate from the slopes of a "lineage-through-time plot" of this kind. The data on Hawaiian silverswords fit the pure-speciation model better than the speciation-and-extinction model (Figure 7.25B), and the per capita rate of speciation estimated in this way was 0.56 species per Myr, a much higher rate than is typical of clades on continents. If a clade continued to increase indefinitely at a rate of 0.5 per year, it would grow from 1 to about 270,000 species in 25 Myr (Nee 2006).

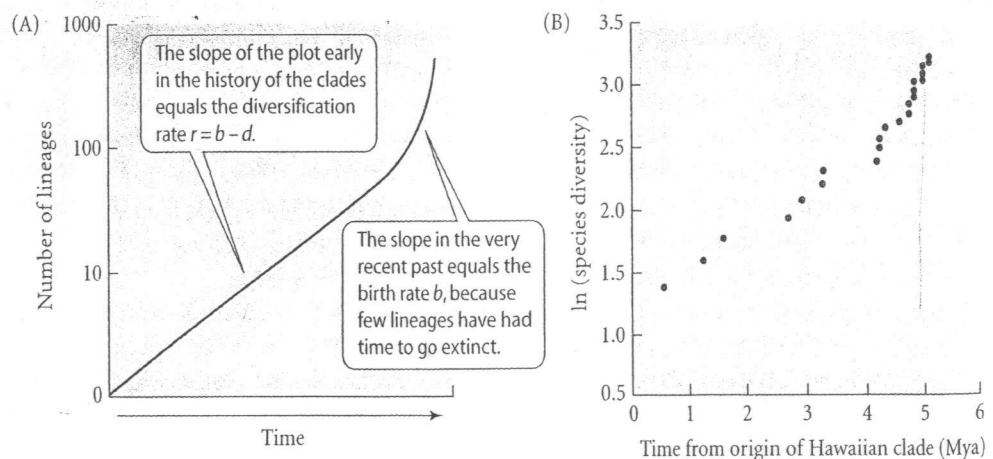
Phylogenetic studies are also central in understanding why some taxa are more diverse than others—why, for example, there are more than 350,000 described species of Coleoptera (beetles) but only 20,000 Orthoptera (grasshoppers and relatives), or why there are fewer than 13,000 species of ferns but about 270,000 species of seed plants. As we have seen (see Figures 7.21, 7.22), sister taxa that differ in species richness must have differed

Figure 7.24 A phylogeny of Hawaiian silverswords, based on rDNA ITS sequences. The divergence between these plants and their closest relatives among the North American tarweeds is dated at 15 Myr. (After Baldwin and Sanderson 1998.)



in the rate of diversification since they are equal in age, and sometimes this rate difference is correlated with a key adaptation. However, Mark McPeck and Jonathan Brown (2007) compiled data from molecular phylogenies of 163 groups of animals in three phyla and found that, in general, species richness is correlated not with diversification rate but

Figure 7.25 Estimating diversification rates from molecular phylogenies. (A) A theoretical lineage-through-time plot of the expected cumulative increase in the logarithm of the number of lineages if rates of “birth” (b) and “death” (d) of lineages are constant. (B) A lineage-through-time plot of the number of lineages of Hawaiian silverswords, based on the phylogeny in Figure 7.24, fits a model of approximately constant speciation rate without extinction. (A from Nee 2006; B after Baldwin and Sanderson 1998.)



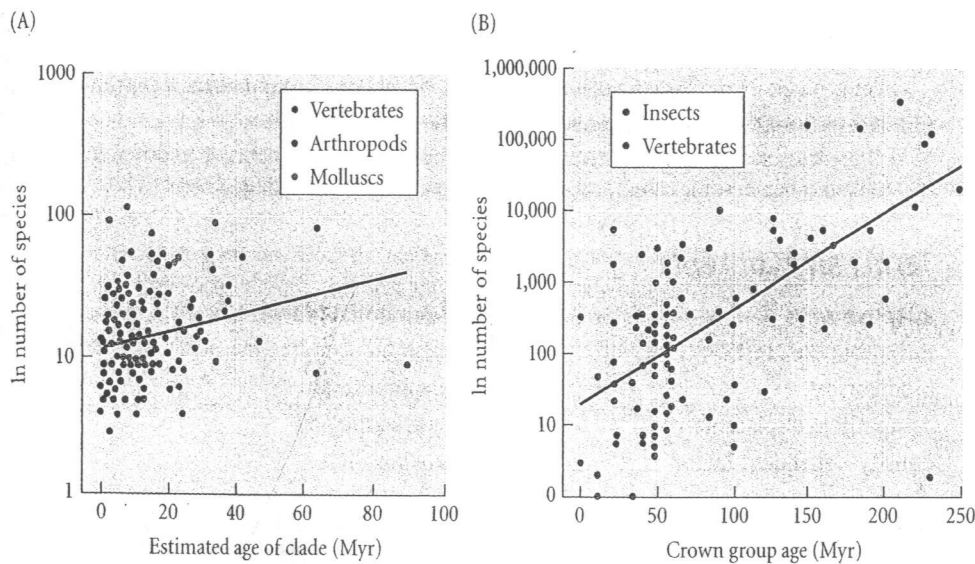


Figure 7.26 The species richness of clades in relation to their age. (A) Data from molecular phylogenies of living species in diverse clades of arthropods, molluscs, and vertebrates. (B) Number of extant species in orders of insects and vertebrates, in relation to age of the order (defined as first appearance of the crown group in the fossil record). These plots, especially of fossil-based data, show a correlation between species richness and clade age. (After McPeck and Brown 2007.)

with the age of the clade, estimated either by time-calibrated sequence differences (Figure 7.26A) or by earliest appearance in the fossil record (Figure 7.26B). Thus, many taxa have more species simply because they are older and have had more time to grow in number.

Summary

1. Analyses of diversity in the fossil record require procedures to correct for biases caused by the incompleteness of the record.
2. The diversity of skeletonized marine animals has increased during the Phanerozoic, but some aspects are uncertain. By direct count of numbers of taxa at each geological stage, diversity appears to have increased in the Cambrian to an approximate equilibrium that lasted for almost two-thirds of the Paleozoic; then, after a mass extinction at the end of the Permian, it appears to have increased (with interruptions) since the beginning of the Mesozoic, accelerating in the Cenozoic. Terrestrial plants and vertebrates show a similar pattern, except that their diversity was relatively stable for much of the Mesozoic. By the Pliocene, the diversity of families and lower taxa was apparently higher than ever before in the history of life. However, recent analyses that account for biases suggest considerably lower post-Permian increases.
3. The “background” rate of extinction (in between mass extinctions) declined during the Phanerozoic, perhaps because higher taxa that were particularly prone to extinction became extinct early.
4. Five major mass extinctions (at the ends of the Ordovician, Devonian, Permian, Triassic, and Cretaceous), as well as several less pronounced episodes of heightened extinction rates, are recognized. Although the cause of the incomparably devastating end-Permian extinction is unknown, it may have been the result of a rapid episode of major environmental changes initiated by the volcanic release of vast quantities of lava. The impact of a large extraterrestrial body at the end of the Cretaceous may have caused the extinction of many taxa, including the last of the nonavian dinosaurs.
5. Broad geographic and ecological distributions, rather than adaptation to “normal” conditions, enhanced the likelihood that taxa would survive mass extinctions. The diversification of many of the surviving lineages was probably released by extinction of other taxa that had occupied similar adaptive zones. Newly diversifying groups have sometimes displaced other taxa by direct competitive exclusion, but more often they have replaced incumbent taxa after these became extinct.
6. The increase in diversity over time appears to have been caused mostly by adaptation to vacant or underused ecological niches (“ecological space”), often as a consequence of the evolution of key adaptations, and by increasing provinciality (differentiation of the biota in different geographic regions) owing to the separation of land masses in the Mesozoic and Cenozoic and the consequent development of greater latitudinal variation in climate.

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7. The rates of both extinction and origination of taxa have been diversity-dependent. Such observations imply that diversity tends toward an equilibrium. However, an equilibrium can change over geological time because of changes in climates and the configuration of continents, and because organisms evolve new ways of using habitats and resources.
8. Differences among taxa in contemporary species richness are attributable to different rates of diversification in some cases, and simply to differences in clade age in others.

Terms and Concepts

adaptive zone	exponential growth
background extinction	incumbent replacement
biodiversity	key adaptation
competitive displacement	mass extinction
density-dependent factor	provinciality
diversification rate	pull of the Recent
diversity-dependent factor	Red Queen hypothesis
ecological space	

Suggestions for Further Reading

Most of the topics in this chapter are treated clearly in an excellent textbook on paleobiology, *Principles of Paleontology* (third edition) by M. Foote and A. I. Miller (W. H. Freeman, New York, 2007). See also D. Jablonski et al. (eds.), *Evolutionary Paleobiology* (University of Chicago Press, 1996). The end-Permian mass extinction is the subject of a popular book by D. H. Erwin, *Extinction: How Life on Earth Nearly Ended 250 Million Years Ago* (Princeton University Press, Princeton, NJ, 2006), and the consequences of mass extinctions are reviewed by R. K. Bambach, "Phanerozoic biodiversity mass extinctions," *Annual Review of Earth and Planetary Sciences* 34:127–155 (2006) and D. Jablonski, "Mass extinctions and macroevolution," *Paleobiology* 31 (Supplement):192–210 (2005).

A thoughtful and informed work about the future of biodiversity is found in E. O. Wilson's *The Diversity of Life* (W. W. Norton, New York, 1999). The same subject is discussed in a more academic manner in *Principles of Conservation Biology*, edited by M. J. Groom, G. K. Meffe, and C. R. Carroll (Sinauer Associates, Sunderland, MA, 2006).

Problems and Discussion Topics

1. Distinguish between the rate of speciation in a higher taxon and its rate of diversification. What are the possible relationships between the present number of species in a taxon, its rate of speciation, and its rate of diversification?
2. What factors might account for differences among taxa in their numbers of extant species? Suggest methods for determining which factor might actually account for an observed difference.
3. Ehrlich and Raven (1964) suggested that coevolution with plants was a major cause of the great diversity of herbivorous insects, and Mitter et al. (1988) presented evidence that the evolution of herbivory was associated with increased rates of insect diversification. However, the increase in the number of insect families in the fossil record was not accelerated by the explosive diversification of flowering plants (Labandeira and Sepkoski 1993). Suggest some hypotheses to account for this apparent conflict, and some ways to test them.
4. A factor that might contribute to increasing species numbers over time is the evolution of increased specialization in resource use, whereby more species coexist by more finely partitioning resources. Discuss ways in which, using either fossil or extant organisms, one might test the hypothesis that a clade is composed of increasingly specialized species over the course of evolutionary time.
5. In several phyla of marine invertebrates, lineages classified as new orders appear first in the fossil record in shallow-water environments and are recorded from deep-water environments only later in their history (Jablonski and Bottjer 1990). What might explain this observation? (Note: No one has offered a definitive explanation so far, so use your imagination.)

6. The analysis by McPeck and Brown (2007) suggests that clades with few living species may be very young. Is this necessarily the case? Are there alternative hypotheses? Can you find evidence for any of these hypotheses? What would constitute evidence?
7. The method of replicated sister-group comparison of species richness has been used to implicate certain adaptive characteristics as contributors to higher species richness. Is there any way, conversely, to test hypotheses on what factors may have contributed to the decline or extinction of groups?
8. Scientific debate continues about the history and interpretation of the diversity patterns of many taxa. Analyze such a debate, and decide whether either side has settled the issue. If not, what further research would be needed? An example is whether or not the enormous diversity of leaf beetles (Chrysomelidae) is due to a long history of co-diversification with their host plants. See Farrell 1998, Farrell and Sequeira 2004, and Gómez-Zurita et al. 2007.