SYNTHESIS

Paleontological Patterns, Macroecological Dynamics and the Evolutionary Process

Bruce S. Lieberman · William Miller III ·
Niles Eldredge

Abstract Here we consider evolutionary patterns writ large in the fossil record. We argue that Darwin recognized but downgraded or de-emphasized several of these important patterns, and we consider what a renewed emphasis on these patterns can tell us about the evolutionary process. In particular, one of the key patterns we focus on is the role geographic isolation plays in fomenting evolutionary divergence; another one of the key patterns is stasis of species; the final pattern is turnovers, which exist at several hierarchical scales, including regional ecosystem replacement and pulses of speciation and extinction. We consider how each one of these patterns are related to the dynamic of changing ecological and environmental conditions over time and also investigate their significance in light of other concepts including punctuated equilibria and hierarchy theory. Ultimately, we tie each of these patterns into a framework involving macroecological dynamics and the important role environmental change plays in shaping evolution from the micro- to macroscale.

B. S. Lieberman (✉)
Department of Geology, University of Kansas, 1475 Jayhawk Blvd., 120 Lindley Hall, Lawrence, KS 66045, USA
e-mail: blieber@ku.edu

W. Miller III
Geology Department, Humboldt State University, 1 Harpst Street, Arcata, CA 95521, USA
e-mail: wm1@humboldt.edu

N. Eldredge
Division of Paleontology, The American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA
e-mail: epunkeek@amnh.org

Introduction

Part 1: History and Nature of the Problem

Empirical patterns form the observational backbone of all of science, including evolutionary biology. As Ghiselin (1987) once remarked in a criticism of Mayr's (1982) claim that there are no laws (regularities, patterns) in historical science, allopatric speciation is such a law; Ghiselin was saying that case after case shows that the vast majority of new species are derived from ancestral species through a process of geographic isolation. The cases are so numerous and so similar as to constitute a great regularity or generalization—whether it be termed a ''law'' or more neutrally, a ''pattern.''

Many of the disputes in evolutionary biology have revolved around what patterns are to be taken as real, and thus of necessity folded into a single, coherent theory of the evolutionary process. The three patterns singled out here—geographic isolation, stasis and cross-genealogical turnover events—have been shunted aside to varying degrees ever since Darwin's epochal *On the Origin of Species* (1859).

The goal of this essay is to evaluate the status of these three patterns in contemporary evolutionary theory; to develop a more coherent process theory of turnover events (the role of isolation and the causes of stasis are already comparatively well understood; see Mayr, 1963 for a discussion of the former and Eldredge et al., 2005 for a discussion of the latter); and finally to demonstrate that the ultimate causal controls in evolution emanate, not from the

genome, nor from environmental components of natural selection, but rather from the internal dynamics of ecosystems when critical points are reached through external physical environmental factors. Such processes are inherently cross-genealogical—resulting in biogeographic range changes, extinction and evolution of new taxa at the species level. Absent such events, within-population selection and genetic drift are the higher order determinants of evolutionary stasis and change; genomic level processes operate independently of such higher level population processes (as Dobzhansky made very clear in 1937: 11) and seldom override the higher level processes. We would argue that, far from being driven by the genome, evolution is a top–down process where higher-level phenomena set the context for the operation of lower-level processes. The greater the magnitude of the higher-level phenomena, the greater the evolutionary effect. However, it is true that lower level processes can in principle penetrate to higher levels and sometimes do. For example, we recognize that evolutionary developmental biology or evo-devo is an important new field with significant implications for our understanding of evolutionary patterns and processes (e.g., Hall, 2003). Still, given the types of data we present and evaluate here, this significant research field cannot be covered to the extent it deserves.

Darwin's Evolutionary Patterns

Darwin discovered three biological patterns while on the *Beagle* voyage between 1831 and 1836 that led him to the notion of evolution (see Eldredge, 2005, for four specific citations of these patterns by Darwin as ''origin…of all my views,'' and for detailed analysis of Darwin's early notebooks and unpublished manuscripts). Each of these patterns involved the replacement of one species by another closely similar (''allied'') form, whether stratigraphically, geographically over large continental areas, or microgeographically on island groups, with isolation an obvious factor in generating divergence. Generalizing from just a few cases, he thought these patterns were best explained by a natural process of emergence of new species from older ones; rather than by the traditional creationist view of Divine Design. Why, for example, would the Creator replace an extinct sloth with a modern one in South America—the Americas being the only place where edentate mammals are to be found? Why would the Creator replace the common rhea with the lesser rhea over the South American landscape—rheas being known only from there? And why would God make four separate species of mockingbirds on the Galapagos Islands—species, moreover, that are all very similar to the mockingbirds of South America? Biogeography and the replacement of one ''allied'' form by another were the common denominators of these three initial patterns.

On his return to England, Darwin opened up his ''Red'' and ''Transmutation'' notebooks (Barrett, Gautrey, Herbert, Kohn, & Smith, 1987). Already a convinced evolutionist by the time the notebooks were begun, Darwin discussed these initial three patterns, and added three more: classification (the Linnaean hierarchy), homology (''unity of type'') and embryology, as additional evidence that life must have evolved. He saw himself as a Baconian inductivist—a view borne out by his *Beagle* experiences, where he was in the process of trying to bring forth in his conscious mind the patterns that he had at first intuited.

But by the time he was back in England and writing his notebooks, Darwin had in fact stopped compiling additional examples from the literature simply to further establish his patterns: rather, he combed the literature for further examples, treating them as ''expectations'' (i.e., predictions) if ''my theory'' (i.e., of evolution) were true. He was testing his idea in good hypothetico-deductive manner: *If evolution happens, this is what you would expect to see*—new fossil species replacing extinct ones; closely related species replacing one another geographically; differentiation of species on islands; a nested pattern of similarity linking up all taxa on earth; the closely related prediction of homology—as in the same basic structure of the forelimbs of tetrapods; and the increased resemblance of embryos within major groups when progressively early stages are compared. All became predictions, sometimes relegated to the status of secondary evidence in support of evolution. But (especially the initial three) were the patterns that originally got him to the idea of evolution in the first place.

And then Darwin discovered natural selection (Notebook D, 1838). ''My theory'' came instantly to mean not just ''evolution,'' but rather ''evolution through natural selection.'' Darwin decided to rederive his original patterns from his notion of how natural selection works (Eldredge, 2005). That's when the trouble started: by that we mean the de-emphasis of well-documented patterns of geographic isolation, species level stasis, and turnover.

Three Patterns that Darwin Downgrades, Dismisses, or Denies

Darwin found three basic patterns incompatible with his idea of how natural selection works to modify species through time:

Isolation

''Although I do not doubt that isolation is of considerable importance in the production of new species, on the whole I am inclined to believe that largeness of area is of more importance, more especially in the production of species,

which will prove capable of enduring for a long period, and of spreading widely.'' (Darwin, *Origin*, p. 105).

In his earlier notebooks and unpublished manuscripts, Darwin was inclined to attribute much greater significance to isolation as a factor promoting evolutionary change than in his later, published views; the shift in Darwin's views is treated in detail in Grinnell (1974), Mayr (1976), Kottler (1978), Sulloway (1979), Kinch (1980), Richardson (1981), Browne (1983), Lieberman (2000), and Eldredge (2005); but some general discussion is useful here. In particular, based on detailed studies of the Darwinian notebooks (Barrett et al., 1987), scholars have concluded that between 1837 and 1844 Darwin subscribed to a view more in line with a geographical, isolationist model of speciation, for instance, noting the important role that geographic barriers play in checking the free movement of groups and in serving to isolate different groups. In 1842 he also commented on how repeated episodes of elevation and subsidence might join and sunder island archipelagos and their associated floras and faunas, thereby leading to divergence (Browne, 1983; Grinnell, 1974; Sulloway, 1979). There is actually some debate in fact as to what role isolation played in generating evolutionary change in these early writings of Darwin. For example, even early on it may have been that the primary role he ascribed to isolation was as a way of subjecting organisms to new selective milieus; Darwin may have also argued that the primary divergence occurred after organisms had been brought back together following isolation (Lieberman, 2000). Thus, even during the 1837–1844 interval Darwin may have attributed less importance to isolation, in and of itself, as a mechanism generating evolutionary divergence than other authors like Hooker (1853) and Wallace (1855, 1857, 1858). Moreover, Darwin was not the first scientist to assert that geographic isolation played a significant role in what we now call speciation: Von Buch (1825) may deserve this honor. Still, Darwin's early focus on geographic isolation dwindled even further after 1844.

There were always a handful of biologists throughout the remainder of the 19th and into the early 20th Century who insisted on the importance of evolution—Wagner, Romanes, Jordan and Gulick to name but four. But, as is well known, it was not until Dobzhansky (1937) and Mayr (1942) focused on the nature and mode of origin of species (defined as reproductive entities, or discrete packages of genetic information) that the importance of isolation was fully established in modern evolutionary discourse. Yet it is still possible today to encounter lengthy treatments of evolutionary theory that entirely ignore the importance of isolation in both the generation and conservation of adaptive evolutionary change. The battle to reinstate the importance of isolation in the evolutionary process, it seems, has not entirely been won even now, yet it has

extremely important implications for our understanding of evolution. In particular, when speciation occurs in the allopatric mode it consigns an important role to geology and climate as the pacemakers of evolution. This is because geology and climate can generate geographic barriers that isolate populations of species, promoting divergence and eventually speciation. At times geology and climate are secondary motivating forces: they do not cause the initial isolation and the organisms actively move over pre-existing barriers, thus becoming isolated. At other times geology and climate are the primary motivating forces and the organisms passively remain in place as geographic barriers are created within existing species' ranges, ultimately leading to isolation and speciation. If this is primarily the way evolution happens, the way Darwin and several other 19th Century scientists predicted, and the way most scientists accept today, then speciation and macroevolution are largely caused by Earth history changes. That is, a sequence of geologic or climatic changes contribute to a sequence of biological changes. If so, then evolution becomes about contingency, using the term from Gould (1989; see Lieberman, 2000). By contrast, with a view of speciation not driven by isolation and instead operating in the sympatric mode, evolution is more about active biological processes including competition.

We note that there is an interesting parallelism between the evolution of Darwin's ideas on speciation, from allopatry and sympatry, and the evolution of the field of evolutionary biology in the latter part of the 20th Century. For example, before 1844 Darwin viewed climate and geology as important evolutionary forces because they led to evolutionary isolation. In this perspective organisms play a more passive role in biological evolution. Later, Darwin came to ascribe a more active evolutionary role for organisms, emphasizing his principle of divergence, with migrations bringing new species into contact with one another, causing selection and precipitating divergence. Through time, a similar switch from a more passive to a more active view of the role of the organism in evolution has occurred in theoretical writings on evolutionary biology. Eldredge (1995) recognized that the original view of natural selection in the Darwinian synthesis (e.g., see Eldredge, 1985) was as a passive form of book keeping. Later, in reformulations by Dawkins (1976), the vision of natural selection, especially as it focused on reproduction leading to the propagation of genes to future generations, was treated, incorrectly, as an active biological force (Eldredge, 1995).

Stasis

''My very theory requires each form to have lasted for its time: but we ought in same bed if very thick to find some

change in upper & lower layers—good objection *to my theory*'' (Darwin, 1838, Transmutation Notebook E, p. 6).

Darwin knew about stasis—as did all paleontologists of his day; Hull (1973) has printed a selection of reviews of the *Origin*—several by paleontologists who raise the difficulty of stasis to the picture of slow divergence that was Darwin's main image of evolution by the time he published the *Origin* in 1859. Darwin, as has been well documented, invented the useful field of taphonomy to explain away the discrepancy between what his theory predicted one should see in the fossil record, and what one actually encounters there. It is our view that it is often questionable to assert that a theory should ever trump actual data collected, although we recognize that theory can color the collection and analysis of data (see discussion in Eldredge & Gould, 1972).

In his essay detailing the history of Darwin's thinking on isolation, Sulloway (1979) reviews the correspondence between Darwin and Moritz Wagner. Wagner read the *Origin*, became convinced of evolution, and was especially struck with the importance of isolation. According to Sulloway, Wagner developed a vision of the evolutionary process that saw isolation as the prerequisite to rapid adaptive change in small populations; if the newly differentiated daughter species survives and expands its range, the rate of evolution would slow to a crawl because of interbreeding throughout the range of a large number of individuals. Thus, apparently on first principles, with no close knowledge of the fossil record, Wagner formulated ''punctuated equilibria'' in the 1870s. A century later, paleontologists finally began to take empirical patterns in the fossil record seriously—starting with stasis (Eldredge, 1971; Eldredge & Gould, 1972). The notion of punctuated equilibria hinges on two patterns: isolation as an important component in generating adaptive change and speciation, plus stasis. It could not have been formulated, in other words, until Dobzhansky and Mayr had first reformulated the importance of isolation.

Wagner utilized a primitive version of what later became known as ''gene flow'' to predict stasis—the characteristic lack of accrual of significant amounts of further adaptive change once a species is solidly established. However, Ehrlich and Raven (1969) called into question the prevalence of gene flow and its putative homogenizing, stabilizing effects on species. In a recent review of the problem, a pluralistic group of geneticists and paleobiologists concluded that stasis is primarily the outcome, not of the stabilizing effects of gene flow, nor of stabilizing selection—but rather the opposite: the disparate, quasi-independent evolutionary histories of different populations of a widespread species living in disparate ecological systems, and thus subjected to somewhat different selection regimes, in addition to different mutational histories

(Eldredge et al., 2005). This view is implicit in aspects of Wright's (e.g., 1931) ''shifting balance'' theory, the net effect of these different evolutionary histories in populations over the entire range of a widespread species is to cancel each other out. Put another way, the probability that directional natural selection can act on an entire species (as if it were, in fact, a single panmictic population) is vanishingly small.

If punctuated equilibria served the dual purpose of integrating existing evolutionary theory centered around allopatric speciation and natural selection, with a long overdue recognition of the prevalence of stasis as an empirical pattern in the fossil record, it also perpetuated a tradition in evolutionary thinking that goes straight back to Darwin: Virtually all analyses of the evolutionary processes—whether or not incorporating speciation theory—focus on the evolution of individual lineages. In most evolutionary studies, with the work of Vrba (e.g., 1980, 1985, 1992, 1995) a notable exception, it is as if evolution of one species occurs in a vacuum relative to other co-existing species. The focus of evolutionary biology has traditionally been on new species within a lineage variously evolving, surviving (with further change or not), perhaps giving rise to descendant species, and eventually becoming extinct—all without regard to the similar classes of events occurring in other lineages, often at more or less the same time. This brings us to the third pattern—where much analytic work remains to be done.

Turnovers

''If species really, after catastrophes, created in showers over world, my theory false'' (Darwin, 1844, *Essay*, in F. Darwin, 1909, p. 145).

In the *Origin* (Ch. 10 of the first edition—second geologic chapter of the sixth edition), Darwin remarked that ''groups of species follow the same general rules of appearance and disappearance as do single species''; the groups in question, however, are ''genera and families.'' Darwin is steadfastly and wholly genealogical in his viewpoint in all his published discussions of the evolutionary processes. The ''species created in showers'' quote was a later annotation in an unpublished manuscript—the clearest passage acknowledging that some paleontologists, at least, saw synchroneity in the extinctions and appearances of unrelated species.

For instance, Darwin had read Cuvier, and in his 1812 *Discours*, Cuvier had recognized 33 ''revolutions'' in the history of life as seen in the fossil record. Each revolution was an episode of extinction followed by an act of independent creation. And while Cuvier's explanation for these creations was religious rather than naturalistic,

nonetheless the empirical pattern of turnovers he described and attempted to explain are recognized to have been real.

Yet these cross-genealogic turnover patterns have been almost systematically ignored. Lyell's success in establishing uniformitarianism as a more useful and productive conceptualization of earth history than catastrophism helped relegate Cuvier's perceptions to near oblivion. As Gould (1965) pointed out, uniformitarianism is simultaneously an ontological claim about characteristic rates of geologic process *and* an epistemological recipe for deciphering earth history. Darwin's version of evolution—emphasizing gradual divergence of species—was in many ways the biological parallel to the ontological side of Lyell's uniformitarianism. Darwin never pursued his worries about near-synchronous cross-genealogic species disappearances and appearances; he simply quietly dropped the matter altogether.

Turnovers such as Cuvier described, long before Darwin, have been ignored at least as much as stasis in all the years since Darwin published the *Origin*. Newell (e.g., 1967) was the first modern scientist to take mass extinctions to be real phenomena, worthy of analysis in their own right. Describing them variously as ''crises''—or, following Cuvier, as ''revolutions''—Newell bucked the uniformitarian tide, with its insistence upon seeing earth and biotic history through the prism of gradualism.

The discovery and cataclysmic interpretation of the end-Cretaceous iridium layer (Alvarez, Alvarez, Asaro, & Michel, 1980) finally brought mass extinctions the attention that they deserved. Mass extinctions clearly have happened, and just as obviously have had major effects on the subsequent evolution of life by pruning entire clades of higher taxa, and thus subsequently allowing once subordinated clades to come to the fore as documented by Gould (1989, 1996), Raup (1989) and others.

Transitioning from the largest scales to much smaller scales, equally well empirically established are localized ecological disturbances, often resulting in the deaths of many (sometimes all) of the local inhabitants in that area. The ecological effects of forest fires, volcanic eruptions and the like have been well studied for at least a century. The general process of succession through recruitment from outlying demes of species that had been represented in the disturbed fauna usually results in restoration of an ecosystem that could be virtually identical to the state it had been in prior to the disturbance. Because little or no significant evolutionary change accompanies these events, events of localized disturbance and recovery have not been integrated into evolutionary theory. They should be—for it is clear that there is strong empirical evidence for ecological disturbance on the smallest scale, just as on the grandest spatiotemporal scales.

Just as there are documented ecological disturbances at the smallest and largest scales, it is a natural prediction that there should be events intermediate in scale—events that encompass sufficient geographic range as to effect entire species—not merely localized demes, but, then again, not sufficiently large in scale to embrace numerous clades of higher taxa. The effects of these intermediate events might be predicted to parallel the largest (and smallest) level events. Instead of driving clades (or demes) to extinction, and facilitating the later evolution of other clades (or demes), they might cause species extinction and subsequent speciation. What the threshold separating smallest, intermediate, and largest events is has not as yet been specified. The prediction is that there should be events in the history of life sufficiently large to reach a threshold effect—driving many species in the regional biota to extinction, and causing others to undergo speciation (Fig. 1).

Beginning in the mid-1980s, paleontologists finally began taking these events seriously. Vrba (1985), for example, proposed her ''turnover-pulse hypothesis'' based on her analysis of the events culminating ca. 2.5 Ma in eastern in southern Africa. Later, Brett and colleagues (e.g., Brett & Baird, 1995) proposed their related model of ''coordinated stasis'', based on the sequence of appearance and extinction of eight biotas in the mid-Paleozoic of eastern North America. Brett and Baird (1995) recognized that several different fossil lineages that occurred in the same region showed a hallmark feature of punctuated equilibria, stasis; moreover, these species tended to turnover and go extinct in concert.

Based on these patterns, spanning disparate time scales and distinct groups, we would argue that the pattern of regional biotic turnovers is real. In fact, the pattern is the basis
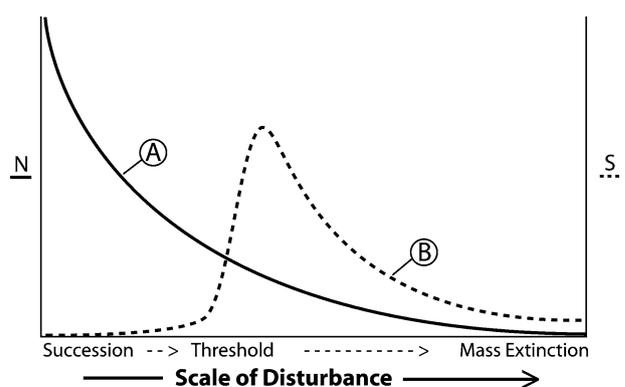

Fig. 1 A representation of the relationship between frequency and scale of disturbances (**A**) and the possible accumulation of adaptive speciation through the Phanerozoic (**B**). Minor, localized disturbances causing succession and related changes (Miller, 2000b) are millions of times more common than global mass extinctions (N), but most of the fully differentiated and reproductively isolated species (S) probably emerge at the threshold where regional ecologic systems are reorganized or replaced. (From Miller, 2004, Fig. 1)

for the zonation of the fossil record. We would argue that it is time to take this pattern of turnovers at the intermediate level very seriously. The phenomenon of mass extinction has received significant attention from paleontologists, and deservedly so, but further investigation of these intermediate turnovers may confirm the notion that during the history of life by far the greatest number of species extinctions and speciation events have taken place in near synchronicity. That means that most of the adaptive change through natural selection and drift that has occurred in the history of life could have happened during turnover events.

The turnover pattern is not just a random collection of extreme events that have periodically come along to disrupt the ''normal'' course of evolutionary history. Far from it: without them, there would be no evolutionary history to speak of. It is imperative that these patterns be recognized, modeled and analyzed—not just by paleobiologists, but also by all evolutionary biologists who truly seek a deeper understanding of the evolutionary process.

In a sense Darwin was right when he saw that stasis was a valid objection against his theory—and when he stated so starkly that ''if species really, after catastrophes, created in showers over world, my theory false.'' But his theory is not false; as was true of isolation, and later stasis, the patterns must be recognized, taken seriously, and then integrated with Darwin's view of evolution through natural selection.

But Darwin was right to see that his theory would look very different were these higher-level phenomena of isolation, stasis and turnovers admitted into the list of patterns that need to be incorporated into evolutionary theory. After all, early discoveries in genetics suggested to many biologists that, now that the physical basis for understanding why organisms resemble their parents, and how genes can be modified through mutation, were beginning to be understood, there was no longer any need to entertain the notion of natural selection. It took Fisher, Haldane and Wright to reconcile Darwinian selection with genetics. And it took Dobzhansky (1937, p. 11) to point out that selection acts on a higher, population level than what he called the ''physiological genetics'' of individuals.

Now, even with the molecular genetics revolution, it has become clear that nothing that has been learned about genetics fundamentally changes Darwin's ideas on evolution through natural selection. That is because Darwin's ideas pertain to higher-level processes that, in a very real sense, pick and choose from what the molecular level presents to it—determining to a large extent what gets passed on at the molecular level.

That is what is so threatening about isolation, stasis and turnovers to Darwin and his intellectual descendants. For these are patterns that bespeak processes that set the context for the action of natural selection. Put another way, a theory that adds isolation, stasis and turnovers, incorporating Darwin's selection, Wright's drift, and everything that has been learned about genetic processes, will indeed look very different from the picture of the evolution of life that Darwin created for us without those three ingredients—a picture that is still so ardently clung to by many contemporary evolutionary biologists.

If such indeed be the case, the conclusion is inevitable: the main causal controls in the evolutionary process are higher-level phenomena. Turnovers of varying orders of magnitude provide the stimulus for reshuffling the genetic deck and provide the context for selection.

Part 2: Ingredients of a New Macroecology and the Dynamics of Evolutionary Turnovers

With the confirmation of the reality of evolution and the establishment of the primacy of natural selection, Darwin (1859) started us on the journey to a comprehensive interpretation of the origin, structure and fate of biological diversity. Later, in the mid-20th Century, cross-disciplinary revivals of evolutionary theory—known collectively as the Modern Synthesis—stressed the importance of population structure, reproductive isolation, geographic context and more generally fracturing of established species as critical ingredients of evolution (Dobzhansky, 1937; Mayr, 1942; Simpson, 1944; see the overview by Eldredge, 1985). This also marks the beginning of the modern controversy over ontological status of species—the ''species problem''—which continues without a consensus solution (Claridge, Dawah, & Wilson, 1997; Hey, 2001; Howard & Berlocher, 1998; Miller, 2001; Wilson, 1999; Wheeler & Meier, 2000). The next major stride in extending theory was the introduction of punctuated equilibria, and especially the establishment of stasis as a primary feature of the history of many species-lineages (Eldredge 1989; Eldredge & Gould, 1972; Gould, 2002; Gould & Eldredge, 1977, 1993). Discussion continues about the prevalence of stasis, the processes that maintain stable species-lineages, and the circumstances surrounding the ''breaking'' of stasis (Benton & Pearson, 2001; Eldredge et al., 2005; Jackson & Cheetham, 1999; Lieberman, Brett, & Eldredge, 1995; Miller, 2003; Stanley & Yang, 1987).

From here the journey that Darwin initiated leads to a superficially and rather selectively explored frontier, consisting of some relatively familiar concepts and problems (environmental pacing, disturbances and ecosystem collapse, clade structure, extinctions and recoveries), and interpretations and ideas that are decidedly less familiar (biological hierarchies, turnover pulses, coordinated stasis, eruption and spread of innovations, pulses of adaptive speciation), intermingled and connected in causal struc-

tures we can barely visualize. The next major strides will advance (and in some sense replace) the Synthesis by including properly scaled ecological processes and patterns, not as backdrops but as essential components in macroevolution; by establishing a more comprehensive and realistic view of the internal structure and status of species; by owning up to the overarching control of the environment (including climate and geologic processes) in species-level evolution; by expanding the role of evo-devo studies (e.g., Cartwright, 2003; Hall, 2003) and by evaluating the relationships between disturbances of varied scale, reorganization/replacement of ecological systems of varied size and kind, and the circumstances producing pulses of adaptive speciation in time and space.

In this section, we discuss what we see as some of the more important landmarks in the frontier region of macroevolutionary theory—critical ingredients in an expanded discussion of species origins and connections to development of ecological systems. The reader will notice immediately that the exploration has as much to do with characterization of entities and levels of organization as it does with interpretation of controls and interactions—as it always has.

What are Species, and Why Does It Matter?

The Lineage Concept of Species

One of the easiest ways to start an argument with either a neo- or paleobiologist—a person who actually deals with whole organisms or aggregates of organisms—is to make a claim about the ''ultimate'' nature of species. There are at least two dozen operational species concepts that have been seriously discussed in recent years (see Mayden, 1997, for an attempt at an inventory). There is a strong flavor of scientific parochialism in this debate: workers in different biological disciplines typically favor their own brand of species concept.

Notwithstanding the continuing differences in opinion, there are certain conceptual elements that most workers would now acknowledge as fundamental properties of species in general. As Eldredge (1985, 1989, 2005) has repeatedly pointed out, at any particular moment in the history of an established species, such entities are best viewed as ''packages of information'' more or less isolated and protected from other such entities. Viewed over time, many theorists acknowledge that species are separate lineages that (1) have beginnings (speciation), (2) unique evolutionary and ecological histories (reflected in the extended internal structure of demes, unique biogeographic histories, and different kinds of ecological ''involvements''), and (3) an eventual termination (lineage extinction); they are simultaneously wholes and parts (in the sense that they contain spatiotemporal networks of demes and at the same time are the parts of monophyletic clades);

and in terms of speciation outcomes, not all species are born (evolutionarily, ecologically) equal. Species are thus the smallest twigs in the tree of life resolvable over geologically significant periods of time. Each has a different history and status; reproductive isolation and strong phenotypic differentiation are characteristics of many but not all lineages, and so are best treated as secondary properties of species. Furthermore, ecology is no longer considered as merely a backdrop, but rather as an essential component of the emergence, life history and extinction of species of all kinds (Miller, 2005).

Further, many operational concepts seem to be homing in on essentially the same ontological target—something like G. G. Simpson's Evolutionary Species Concept (1961: 153), or at least an ultimate picture of species that encapsulates both the genetic autonomy criterion and the fact that species are historical, hierarchical entities (see the recent discussions in Brooks and McLennan, 2002; de Queiroz, 1998; Miller, 2001).

Speciation Pathways and Products

Although the fracturing of established reproductive communities/cohesion systems of some sort, and production of new, independent lineages, seems to be a general property of species emergence, there are few other reliable generalizations that cover all forms of life. The geographic contexts (some version of allopatry, parapatry, or sympatry) and mechanisms (natural selection, sexual selection, drift, and hybridization) are varied (Fig. 2), with modal pathways recognized in only a few well-studied clades (e.g., natural selection + allopatry for fish, birds and mammals; see Lynch, 1989). Considering all plausible scenarios and taxa, neobiologists now paint the following general picture of speciation (McKinnon & Rundle, 2002):

- Speciation is frequently rapid
- Geographic context is diverse
- Speciation involves divergence in many traits
- Divergent selection is the dominant mechanism

Paleobiologists are arriving at a different kind of picture of speciation (Eldredge, 1995; Eldredge & Gould, 1972; Gould, 2002; Lieberman, 1992):

- The fossil record (spatiotemporal distribution) of skeleton-bearing, abundant and widespread species can be read essentially ''literally,'' at least in terms of apparent species-lineage stability
- Most morphologic transitions take place during speciation
- After establishment, many species undergo very little directional change in morphology, sometimes for millions of years

Fig. 2 Relationships between speciation pathways (**A–D**; e.g., allopatry + natural selection as dominant factors in **A**), the varied outcomes of speciation (see the models in Fig. 3), and lineage topology (the ''shape'' of speciation). Although pathways and outcomes (the modes of speciation) may vary, the pattern and hierarchical status of species-lineages is the same for the vast majority of organisms (From Miller, 2006, Fig. 2)
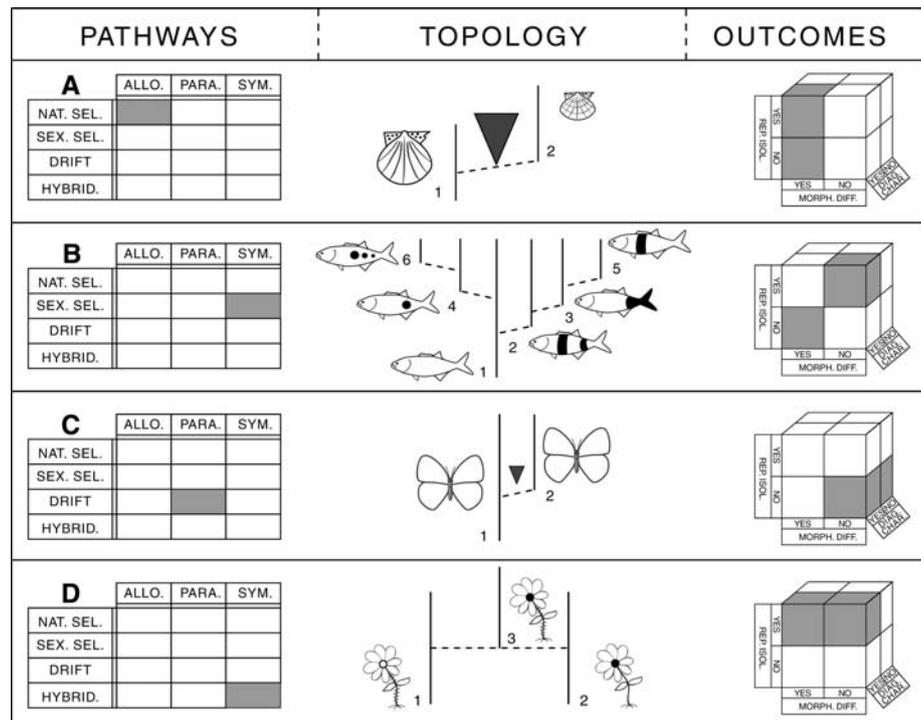
All of the foregoing must add up to a general picture of speciation, but exactly how the neo- and paleobiological perspectives fit together to make a comprehensive theory is not entirely clear. It appears that the picture of species formation, then, will have to be complex and highly individualized, taking into account varied contexts, mechanisms, and—an aspect of speciation that has not been adequately discussed—different outcomes or speciation products. The obvious difference in these two general perspectives is that neobiologists are focused on population processes and patterns, while paleobiologists have a more ''coarse-grained'', temporally extended view of speciation. These pictures have to be complimentary in ways that remain to be fully explored.

Vrba (1985) was one of the first theorists to directly confront the issue of varied outcomes or products of species-level evolution (discussed in Eldredge, 1989; Miller, 2001). Her now familiar figure, pairing morphologic differentiation with speciation (establishment of reproductive isolation in this case), features four possible outcomes, including speciation with strong differentiation as well as speciation producing only slightly differentiated species (cryptic species) (Fig. 3A). A more elaborate view proposing eight possible outcomes (Fig. 3B) was offered by Miller (2001) to cover all conceivable products of speciation. If we are to take these conceptualizations seriously, species may emerge as (1) fully differentiated and reproductively isolated, (2) isolated enough to maintain their autonomy but only weakly differentiated compared to the parent species, or (3) separated in terms of habitat or geographic distribution only, having a few new traits but with no means of isolation in the event contact is re-established with the parent. In the first case, species may potentially go on to dominate ecosystems or at least make up the retinue of dominant species; we do not know very much about what happens in the event of the other outcomes (see the discussion by Cracraft, 1989). In short, there may be an important connection here between the future ecological success of a newly emerged species—reflected in broad geographic distribution, membership in many local ecosystems, large populations at least in some parts of its range—and the modal outcome of the speciation process.

The Connection to Punctuated Equilibria

Several studies have confirmed the widespread occurrence of lineage stasis and punctuation by cladogenesis in the fossil record (reviewed in Benton & Pearson, 2001; Cheetham, 2001; Gould, 2002; Gould & Eldredge, 1993; Jackson & Cheetham, 1999; Lieberman et al., 1995). The stable lineages detected in fossil data sets appear to be, for the most part, species that were abundant, widespread and participants in many local ecosystems. Perhaps the fully differentiated, reproductively isolated product is the kind of species that goes on both to dominate regional economies and to ultimately appear in the record as long-lived, stable lineages. Do cryptic species have this same kind of durability and ecological significance? Are the differentiated and isolated species being produced continuously, or
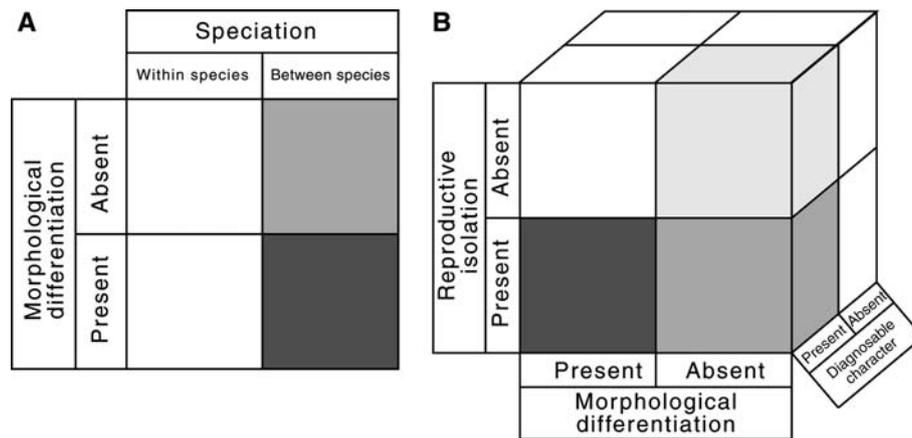
Fig. 3 The possible outcomes of speciation. (**A**) Vrba's (1980, Fig. 5) model relating morphological differentiation and reproductive isolation. (**B**) Miller's (2001, Fig. 2) more comprehensive representation of speciation outcomes, which includes the fully differenti- ated + reproductively isolated products (dark gray), isolated cryptics (medium gray), and cryptics lacking full-fledged isolation (light gray) but featuring diagnosable characters signifying minimal differentia- tion

does their production or accumulation occur in pulses in geologic time? What does it take to achieve the kind of equilibria envisioned by the framers of the theory, and what do ecological patterns and processes have to do with it?

Hierarchical Concept of Ecosystems and Connections to Macroevolution

The Place of Ecology in Evolutionary Theory

In the mid-20th Century, evolutionary theory and ecology developed as essentially separate endeavors, with only a few notable instances of cross-fertilization (e.g., Huxley, Hardy, & Ford, 1954). It has always been fashionable to stress one or the other: from the perspective of those interested in speciation and the nature of species, it was often said that ''evolution occurs on an ecological stage'', thereby underselling for decades a critical ingredient in the potential expansion of the Modern Synthesis by assuming a passive, background role for ecology.

Some theorists are now convinced that macroevolu- tionary theory cannot advance without the incorporation of properly scaled ecological processes and patterns as critical ingredients (Brown, 1995; Eldredge, 1985, 1989; Eldredge & Salthe, 1984; Ivany & Schopf, 1996; Miller, 1996; 2002a; Salthe, 1985; Schluter, 1996, 2000; Thompson, 1998). In this view, ecological systems are construed as historical entities (like demes, species and clades in the genealogic hierarchy), but are concerned with matter + energy processing, not production and conservation of packages of genetic information (Eldredge & Salthe, 1984; Eldredge, 1985; Salthe, 1985). Such economic systems are hierarchically organized: they are

also simultaneously parts and wholes, with interactions at varied focal levels, and across levels with component and encompassing systems (Table 1). Each individual system should have the interrelated properties of (1) *scale* (geo- graphic extent, characteristic rate constants and durations, and hierarchical position), (2) *boundaries* of varied kinds (including gradational versus abrupt), (3) *integration* (quality, quantity, and intensity of connections between internal subsystems), and (4) *spatiotemporal continuity* (initiation of a system, its unique history including disturbances and recoveries, and its eventual collapse) (Salthe, 1985; Miller, 2002a, 2004).

Stability and Change

The evolutionary history of life appears to consist of long intervals characterized by little change, punctuated by much briefer intervals of demonstrable, sometimes dra- matic biological transition (Gould, 2002). Evidence sug- gests that ecological entities also have histories including relatively stable intervals alternating with episodes of dis- turbance and recovery, and that these occur on a broad spatial and temporal spectrum (Miller, 1986, 1996, 2002a, 2004). We acknowledge that when it comes to ecological systems, there is still debate about whether or not local and regional ecosystems can be construed as historical entities. Still, some have argued cogently that larger, regional sys- tems do seem to feature the pattern of stability alternating with rapid change and recovery (DiMichele et al., 2004; Ivany & Schopf, 1996). This level of organization is of special interest to us because of what we see as crucial connections to macroevolutionary processes.

Regional ecosystems experience disturbances and intervals of recovery during which some of the component

Table 1 A hierarchy of ecologic systems

Biosphere system						
	*Province systems					
		*Regional ecosystems				
			*Biotope system (closely connected local systems)			
				Local ecosystems		
					Interaction cells within larger networks	
						Avatars (local population systems)
						Individual organisms and colonies

Each system interacts with similar systems at the same level of organization; its development and organization result from interactions of component systems (working parts) and constraints imposed by the next higher system (the ''ecologic context''). The more inclusive systems tend to be larger, more durable, and feature slower characteristic process rates compared to smaller, component systems. Systems most likely to be directly involved in the kinds of processes we describe are indicated with an asterisk.

local ecosystems undergo replacement, metapopulation networks are reorganized or collapse, and abandonments and invasions start to happen. If the disturbances are severe, waves of extinctions and appearances of new species occur, but the first reaction of component organisms will be to shift populations to more favorable localities (*habitat tracking* of Eldredge, 2003). Regional systems are sometimes pushed to the point of collapse, when environments change quickly and severely, setting off intervals of regional reorganization/replacement involving processes about which we know very little (Miller, 2002a, 2004). This is the level of disturbance where not only regional ecosystems crumble, but also major abandonments and invasions start to happen, along with extinction and—of special interest to us—waves of coincident speciation in different clades. This is a level in the organization of life where economic and genealogic processes become intertwined, in what Vrba (1985) has described as *turnover pulses*, Eldredge (2003) characterized as the middle level of his *sloshing bucket* model of evolution, and Miller (2004) referred to as *macroevolutionary consonance*.

Regional Ecosystem Assembly and Connections to Macroevolution

Regional ecological processes and macroevolutionary patterns are not merely synchronized or have similar spatial scales, but actually seem to be coordinated in certain ways. Species-lineages that are coincident in space and time and

bundled in the same regional ecosystems seem to be mostly the products of a previous interval of reorganization and replacement, or turnover pulse. Explaining the relative stability of both the coincident lineages and the large ecological systems that contain them is one of the great unaddressed problems of modern paleobiology. According to Vrba (1985: 229), the relatively brief intervals of change feature a ''…concentration of turnover events against the time scale. For example, if a high number of first and last records of species in different lineages occur together within a time interval of 100,000 years or less, preceded and postdated by a million years of predominant stasis in the same monophyletic groups, I would regard this as evidence of a turnover-pulse. I expect that turnover-pulses also occur in more refined time intervals, and that at least some stratigraphic sequences will be of sufficient quality to show this.'' What makes this especially interesting is that waves of adaptive speciation are predicted during such intervals of regional disturbance and recovery. Turnover pulses may be the engines for coordinated adaptive speciation in many clades, either in the form of many new species of all stripes appearing at nearly the same time, or in the survival and promotion to ecological prominence of more upstarts or previously rare species, or possibly both. This would be analogous to the proliferation of Paleogene mammals after the demise of the large, non-flying dinosaurs.

Episodes of regional ecosystem reorganization/replacement, and coordinated pulses of extinction and adaptive

speciation, are often caused by environmental changes that disrupt ecological interactions, diminish or eliminate vital resources, and shrink or erase habitats, leading to spatial isolation of population remnants. We expect such changes to simultaneously cause the collapse of many interdependent local systems and regional metapopulations. Some of the major processes that cause these episodes of regional turnover also cause isolation and include: alterations in major geochemical cycles; processes associated directly or indirectly with plate tectonics, including volcanic activity and plate movements; climate change, perhaps related to the former or driven by astronomical cycles; and impacts of comets/asteroids.

Environment as the Primary Control of Macroevolution

Mass Extinctions and Regional Turnovers

Different mass extinction episodes probably involved different ultimate causes, but these causes led to environmental changes that resulted in collapses of biodiversity and ecological systems (Hallam & Wignall, 1997; Wignall, 2004). These are the greatest and most complex disruptions of life on Earth, in terms of: (1) intensity, duration, and scope of the forcing; (2) scale of biological reactions, including extinction of entire clades, worldwide disruption of primary production, and the eradication not just of large ecological systems but of certain *kinds* of systems altogether (e.g., Ausich, 1997); and (3) in terms of length and complexity of recovery intervals (Jablonski, 2004).

For a start, we might hypothesize that regional turnovers are smaller-scale versions of mass extinctions, but with important differences relating to frequency and spatial scale. If regional disturbances and turnovers correspond to most of the minor division boundaries (stages) of the Geologic Time Scale, as suggested by Eldredge (2003)—in a macroevolutionary confirmation of what the biostratigraphers have known all along—it is fairly clear that these disruptions are at least a hundred times more common than mass extinctions. Also, their geographic scale is far more regional, again reflected in the long recognized fact that different biostratigraphic stages may be resolvable in different places. A general question is what type of environmental changes are more likely to cause regional turnovers. We would predict that often climate fluctuation has an important role.

The Importance of Climate Change

Phanerozoic climate change encompasses a broad range of possibly non-cyclical phenomena at the largest temporal scales, like the long icehouse-greenhouse alternations inferred from the Phanerozoic record extending over tens of millions of years; to distinctly cyclical phenomena operating on intermediate to shorter time scales and spanning orbital forcing of climate cycles in the 10^5–10^4 year range; through to Dansgaard-Oeschger Cycles and shorter seasonal and even daily fluctuations (Frakes, Francis, & Syktus, 1992; Huntley & Webb, 1989; Ruddiman, 2001; Vrba, 1992). There is a long tradition of viewing environmental change as one of the prime motive forces of evolution. We note, however, with interest that most of the evolutionary biologists who focused on the role of climate change in evolution were in fact primarily paleontologists. For example, Osborn (1906), and Matthew (e.g., 1915) are among the most well-known exponents of these views, although the paleobotanist Adolphe Brogniart (1829) had among the earliest insights. All of these scientists and their views and conclusions are expertly discussed and evaluated by Bowler (1996). In effect, these earlier views focused on climate change causing migrations, extinctions, and eventually evolution. Related views appear in the Darwinian notebooks (Barrett et al., 1987) and in the writings of Wallace (1876). In spite of these early workers, and their prominence, in the middle part of the 20th Century the role of climate as a motive force of evolution was de-emphasized. One of the major workers who demonstrated how important it was to reconsider the role of climate in evolution was Elisabeth Vrba (e.g., 1980, 1985, 1992, etc.) in a series of detailed studies including those already described in relation to the turnover pulse hypothesis. Huntley and Webb (1989) and Bennett (1990, 1997) have also been among the forefront of scientists that have forced a rejuvenation of ideas on the relation between climate change and evolution.

There are certainly parallels between the ideas of these more recent scientists and the earlier practitioners already mentioned. For example, each of these authors recognized that climate change often caused biogeographic range change as an initial consequence; and this in turn would lead to extinction and speciation. There is, however, we believe, a more than subtle distinction between the more modern treatments such as those of Vrba and the earlier ones of Matthew and Osborn. This is because authors like Matthew and Osborn primarily invoked interspecific competition as the mechanism that leads both to extinction and speciation after new types of organisms come into contact with one another. By contrast, Vrba recognized that the primary factor causing extinction and speciation was the isolation and associated reduction in population size *itself*. The difference between a process view based on competition and one centered on the contingency of isolation is an important one, and harkens back to the distinction we made earlier between views of evolution that centered on either the sympatric or allopatric modes of speciation.

Distinguishing the Primary Evolutionary Factors: Geology Versus Climate

Many of the early scientists already mentioned including Osborn, Matthew, and Brogniart, but also Huxley and Wallace, were prescient enough to recognize that it was often geologic change that triggered climatic change and both in turn strongly influenced the course of evolution. In such a situation, clearly both geology and climate are interrelated evolutionary factors and it is impossible to dignify one, or the other, as of utmost importance. Sometimes, however, it is conceivable that one of these factors played the primary role in leading to geographic isolation that caused speciation or extinction. Thus, a useful question is how is it possible to distinguish between geologic and climatic change as the primary factors motivating evolutionary divergence in a given group of organisms in a given region at a given time (see discussion in Hallam, 1981).

Phylogenetic biogeography offers one way of distinguishing the relative importance of these two factors. Many clades show a phylogenetic biogeographic signature of congruent episodes of vicariance: that is, patterns of allopatric differentiation across geographic space. Many clades also show a phylogenetic biogeographic signature of geodispersal: congruent episodes of range expansion across geographic space. Cycling or oscillatory episodes of climate change might be expected to produce similarities between the patterns of vicariance and the patterns of geodispersal because they will encourage, at different times, episodes of congruent range contraction and range expansion (Lieberman, 2000, 2003a). Geological processes are not predicted to be cyclical on time scales associated with animal or plant speciation and will not produce repeated episodes of congruent range contraction followed by congruent range expansion. Thus, if phylogenetic biogeographic patterns of vicariance and geodispersal in clades of organisms from particular regions are similar it would be evidence that climate played an important role in motivating evolution. By contrast, if these patterns are different it would suggest that geological changes played the more important role in shaping evolution.

In fact, it appears that at different time periods different forces, i.e., climatic or geologic, appear to play the dominant role in shaping evolution. For example, during the Cambrian radiation, which marks the initial diversification of metazoans in the fossil record, geologic factors appear to have been more important (Lieberman, 1997, 2000, 2003a, 2005). This is at least true in the dominant animals of the Cambrian, the trilobites, which show only limited similarity between their patterns of vicariance and their patterns of geodispersal (Lieberman, 2003a, 2005). By contrast, during the Devonian Period, climatic oscillation, or at least a component related to it, cycles of sea-level rise and fall,

appear to have played the more important role in shaping trilobite evolution (Lieberman, 2003a, 2005). These issues can be considered at even shorter temporal scales with phylogeographic studies (e.g., Avise, 1994).

The ''Sloshing Bucket'' Model of Evolution

Eldredge's (2003) Sloshing Bucket model of evolution acknowledges environmental change as the overarching control of extinction and speciation; it also emphasizes the connections between severity and scope of environmental disturbances and the magnitude of resultant evolutionary effects. The sloshing bucket posits that the bigger the environmental jolt, the grander the ecological and evolutionary reactions. Short-lived, localized disturbances produce succession and similar responses, involving no increases in extinction and speciation rates. The greatest disruptions produce mass extinctions, involving many higher-level taxa over broad areas and in varied locations essentially simultaneously, requiring protracted intervals of recovery and resulting in origination of new clades and major innovations. Intermediate disturbances produce something in between these extremes. The ultimate effects of these may involve reaching or passing unspecified threshold conditions upon which regional ecosystems become reorganized or replaced and concurrent waves of speciation begin to happen (Fig. 1).

This general picture of the causal connections between environment, ecology and macroevolution guides attention to the intermediate levels of disturbance where biogeographic migrations, extinction, and speciation are touched off. ''Only when the threshold is reached and extinction and speciation (correlated, but as yet without complete causal understanding) become dominant elements of response, do we encounter actual evolutionary change to any significant degree'' (Eldredge, 2003: 28). These threshold events are at least hundreds of times more common than the great mass extinctions—forcing the realization that this is where most of the evolutionary action occurs. Acknowledging this pattern as a central feature of the history of life, the question becomes: what exactly happens during reorganization/replacement of a regional ecosystem, and exactly how do these processes of ecological change shape macroevolutionary patterns?

The Structure of Regional Turnovers, and the Timing and Pacing of Macroevolution

What kinds of biological reactions take place in the midst of a turnover pulse? Are these episodes of large-scale ecological reorganization/replacement essentially scaled-up or cumulative versions of small-scale disturbances

(succession, local ecosystem replacement), or are the processes of collapse/reaction unique to this level of organization? Exactly how do regional ecosystems crumble? Although little is known about the structure of turnover pulses, we can anticipate some plausible scenarios.

Disturbance and Reaction at the Scale of Regional Ecosystems

The generalized pattern of collapse envisioned so far includes habitat alteration or destruction setting off abandonments/invasions, extinctions, and speciation (Vrba, 1985, 1993; Eldredge, 1989, 2003; Miller, 2002a, 2004). With regard to the fate of the component local ecosystems, regional systems could undergo the following idealized reactions (see Miller, 2002a, Fig. 4): (1) complete collapse of all component systems and subsequent establishment of a totally new regional ecosystem, having different taxa and a different array of local ecosystems; (2) selective elimination of the most vulnerable local systems, with replacement of just these components in the reorganized ecological regime; (3) down stripping of regional systems by elimination of many component local ecosystems without subsequent replacements; and (4) catastrophic collapse of the regional systems without any immediate replacement or recovery at the scale of local systems (a situation probably more common during mass extinctions when raw material for replacement simply is not available until clades recover sufficiently). A fifth possible outcome is ''none of the above'' if regional systems in certain areas or environmental realms waver a bit during environmental disturbances, at the same time adjacent systems are falling apart, but experience no loss of component local ecosystems.

Another likely impact of change in environmental parameters, too drastic or fast for organisms to react to by means of habitat tracking, would involve rapid elimination of metapopulation networks, viewed as a kind of biogeographic wiring within regional systems (Fig. 4A). In terrestrial systems, population networks often consist of autonomous patches making up the geographic structure of a species (Gilpin & Hanski, 1991). Some of the patches behave as sources of recruits to outlying colonies or local systems recovering from small-scale disturbances, while others (sinks) run a constant deficit and must be subsidized from the source populations (Pulliam, 1996 and references therein). This architecture changes through time, but in a snapshot would have the geometry of discrete patches connected by intermittent migration corridors. Marine and other aqueous population networks may not have exactly the same architecture, especially where environmental gradients and boundaries do not produce the patchiness so typical of terrestrial vertebrate and vascular plant networks. A better picture of a marine metapopulation—during intervals of relative stability within a regional ecosystem—might be a sort of plasmodial network having more or less continuous geographic coverage by individuals near the center(s) of the network (and regional system), with apophyses and corridors ''smeared'' with individuals leading outward to remote colonies, and with patchiness and intermittent contact finally appearing at the margins of a species' distribution. No matter which network geometry characterizes a dominant, abundant species during the good times, the pattern is predicted to ''shrivel-up'' to form a set of isolated, mostly small remnants during a turnover pulse. (This is very similar to the depiction of habitat fracturing and population contraction proposed by Vrba, 1985, Fig. 1). This is exactly the situation that should touch off a wave of allopatric speciation (*sensu* Eldredge & Gould, 1972; Mayr, 1963), so long as the local patches do not shrink too much (see Miller, 2003). Some of these remnants of the former regime could correspond to refugia, with the same species emerging and expanding from these protected areas after the disturbance ends. It is, however, the waves of newly emerging species, or the higher frequency of incipient species survival, that interest us here. Considering the fine structure of the embedded local ecosystems, and their connections at the regional scale, how would turnover pulses be played out? One must first picture the kinds of connections within and among these local systems. This is not hard to do when it comes to a local ensemble of ''avatars'' (local populations viewed in terms of matter-energy flow). The pair-wise interactions familiar to neoecologists are all potentially at work here (commensalism, competition for limited resources, predation, parasitism, and mutualistic connections), in varied combinations, frequencies and intensities depending on the kind of local ecosystem and its stage of development. (These interactions must be placed in complex networks to get an accurate picture of within-system interactions). But how do the ensembles themselves interact with adjacent systems of similar scale? Polis, Power, and Huxel (2004) clearly demonstrated that, in terms of material and energy transfers, many local systems ''leak'' or spill resources into adjacent systems. All one has to do to see an example of this is to walk the margin of a stream and note the trees that have fallen from the bank into the channel. In this case, a riparian system has contributed food and habitat structure to an adjacent lotic system. It is important to note here that it is not so much the avatars that are interacting between local ecosystems as it is the ''raw material'' (not a local population of a particular species of tree, but tree limbs in general as three-dimensional substrates introduced in the stream channel). When local systems are disrupted, and the supply of nutrients or energy is curtailed, damage could spread quickly throughout a regional ecosystem (Fig. 4B). The resulting transition would leave pieces of downgraded,
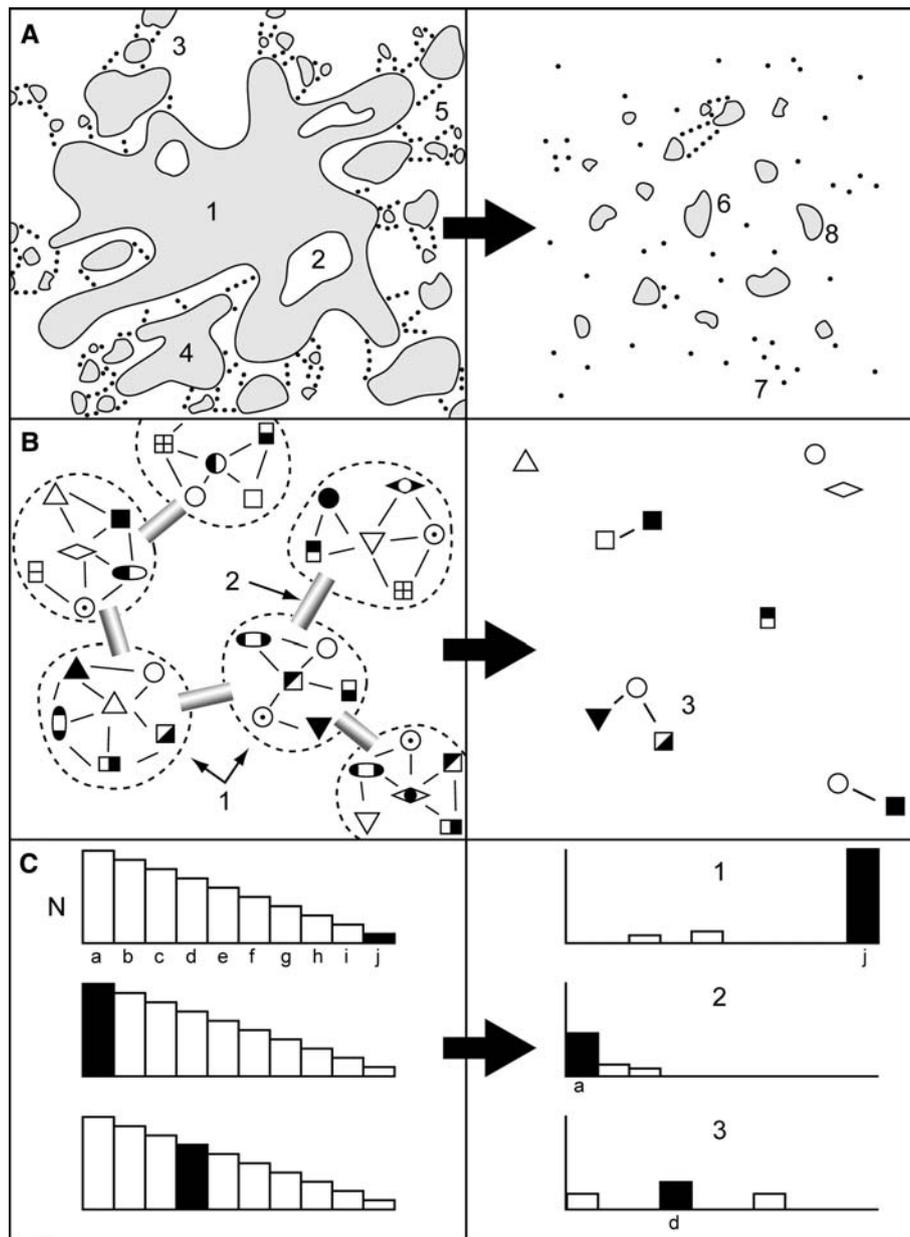
Fig. 4 The collapse of a regional ecosystem viewed in different ways (using different criteria). (**A**) Shrinking and fracturing of species ranges, producing mostly disconnected, remnant patches (**1**, Main body of a large population of marine benthic invertebrates before system collapse. **2**, Temporarily unoccupied space within the main range of the species. **3**, A series of marginal ''sinks'' adjacent to the main ''source'' population. **4**, A large outlier. **5**, Small, ephemeral outliers. **6**, Population remnant near center of the former range, large enough to potentially recover or undergo speciation. **7**, Remnants having the characteristics of population bottlenecks, unlikely to recover or to speciate. **8**, Larger remnant near the edge of the former range, which could potentially undergo an ''Eldredge Pathway'' transformation (Miller, 2003, Figs. 1, 2)). (**B**) Collapse in terms of interaction networks (**1**, Local ecosystems consisting of numerous avatars interacting in different ways and at varied intensities. **2**, Connections between local ecosystems, in terms of material and energy flow. **3**, Remnant of an interaction network.). (**C**) Collapse in terms of species-abundance distributions in the local systems (**a–j**, Species arranged in diminishing rank order in an original local ecosystem. **1**, Promotion of a formerly rare species to dominance. **2**, Reduction to a remnant that retains a ''weak signal'' of the original species-abundance structure. **3**, Reduction to a random assortment of remnants)

disconnected local ecosystems scattered across the landscape. This is essentially the same as the metapopulations shriveling up into isolated remnants, but viewed from a community or ecosystem perspective.

From the point of view of diversity and taxonomic composition, turnovers probably reshuffle the deck in ways that significantly influence recovery patterns (Fig. 4C). The obvious pattern would involve filtering out the ecologically

hypersensitive species, those involved in obligate interactions with vulnerable hosts, and elimination of certain rare species severely reduced in abundance and range already poised on the brink of extinction. During the turnover pulse, previously rare species might rise to dominance, if only briefly, or might give rise to new species that go on to dominate the next regime. Previous dominants could be demoted, surviving the turnover as relatively rare species never again attaining any kind of ecological importance, in terms of controlling or participating in the most important aspects of system structure or function. And in the case of collapse of local systems and elimination of inter-system connections described above, many subordinate or truly rare species might find their status suddenly changed from obscurity to being the ''big fish in a small pond''.

Reorganization/Replacement and Connections to Speciation Rates

We think all of these reactions could produce the conditions and raw material for the replacement or reconstruction of a regional ecosystem. And we are equally convinced that this is where macroecological dynamics and evolutionary processes become intertwined to produce most of the adaptive speciation and species-level innovation of the Phanerozoic (Eldredge, 2003; Miller, 2004). This is not a matter of scaled-up succession and microevolution; migration, extinction and speciation rates are expected to be orders of magnitude higher than those familiar to population biologists—and it also seems that the modal patterns of transition should be different. Threshold effects that we know little about may be at work here (Fig. 1).

As pointed out by Vrba (1993: 431), ''The appearance and removal of barriers to species' distributions is the *sine qua non* of turnover.'' And the shrinking and fracturing of geographic ranges would occur across many taxonomic groups more or less concurrently, owing to simultaneous reaction to environmental forcing and collapse of organizational structures. Therefore, the most significant early reaction, and the one easiest to picture, involves the conversion of species having large, complex distribution patterns with connected populations into isolated pockets scattered across the landscape/seascape, having minimal or possibly no connections to each other. This is the brand of vicariance favored by Vrba as the starting place for multiple episodes of concurrent allopatric speciation in different co-occurring taxa. Populations dwindling to extreme bottleneck conditions, however, are often doomed; the intermediate remnants are the ones preserving a greater (if biased) genetic variation, and are likely to become incipient species (Miller, 2003; Turelli, Barton, & Coyne, 2001). In any case, new species emerge after fracturing of distribution patterns, and this may or may not involve immediate

installment or eventual acquisition of properties of fully fledged species: morphological differentiation and reproductive isolation. Physical separation also has an ecological dimension. The shreds of local ecosystems surviving collapse of regional systems are disconnected from former partnerships and forced into the outer ranges of functional variation. Populations without flexibility and novel options vanish, along with their retinues of predators, parasites and mutualists. One would expect stenotopic species and regional endemics to be especially vulnerable (Vrba, 1985, 1993). We must think of the remnants, together with invaders, as the seeds of new regimes.

After fracturing, shrinkage and disconnection of populations belonging to varied species, how exactly are the subsequent ecological systems inaugurated or reconstructed, and what happens to secure the relative stability of the newly formed ecological and evolutionary entities—one of the dominant patterns displayed by the fossil record (Eldredge, 2003; Eldredge & Gould, 1972; Gould, 2002)? The raw material will now consist of invaders, newly emerged species (of varied status in terms of differentiation and reproductive isolation), and super-eurytopes or organisms emerging from local refugia. We might also consider the patterns of species extinction and regional abandonments as a kind of raw material, too, as these also influence the processes of ecological recovery and the fates of invading organisms, new species and innovations (see the discussion of raw material of regional ecosystem recovery and pulses of adaptive speciation in Miller, 2004: 632–634).

Miller (2002a: 150–151) has suggested three very generalized pathways of reorganization/replacement, featuring different combinations of large-scale ecological and evolutionary processes, framed as questions:

- Does evolution come first?—In this scenario turnover involves a shift in modes and rates of speciation caused (in a proximal sense) by the relinquishing of large amounts of ecospace resulting from wholesale extinctions and abandonments, reduction of species ranges to disjointed patches, and invasions by opportunistic species. Eurytopic species would appear and spread first, and these would give rise to a swarm of new stenotopic species, both of which go on to provide the populations in the newly organized local ecosystems. In this model, the new species and innovations come well ahead of elaborations and geographic deployments, making reorganization/replacement a result of primary, coincident evolutionary reactions. Subsequent stability in the regional ecosystems is the result, then, of emergence of stable species-lineages having large, more or less connected populations (new metapopulation networks) distributed in different local ecosystems (i.e., differing selection regimes).

- Does ecology come first?—In this view, the leftovers (toughest of the eurytopes, species with durable ''resting stages'', organisms hiding out in refugia) and the invaders reorganize/replace the original system, rather like a large-scale version of succession. This implies that not only key species may survive, but that large parts of interaction networks might remain intact in protected places. As long as sources of recruits survive somewhere, the regional system can be rebuilt without an early pulse of adaptive speciation; evolutionary adjustments could come later, however, involving transformations of both the survivors and invaders.

- Do both evolution and ecology come first?—in this view, turnover pulses are experienced by populations as episodes of resource curtailment and habitat fragmentation/elimination, with remnants separated and downgraded in quality. Both evolutionary novelties and invaders can become established as the old ecological regime is swept away. The key difference in this model is that the initial evolutionary and biogeographic changes produce incipient ecological structures, which immediately begin to constrain and promote ongoing invasion, extinction and especially speciation. The vicariant patterns produced by environmental changes produce waves of speciation, and the upstart ecological systems go to work right away to sort the raw material into stable patterns, without any real delay or separation between evolutionary and ecological processes. Miller (2002a: 151) described intermingling of speciation and establishment of new regional ecosystems as ''…being like a tool die that stamps the form of the future, stable system out of the raw material of speciation during turnover pulses''.

The few theorists who have explored this territory seem to favor a scenario like the last one, in which large-scale ecological processes and speciation pulses go hand-in-hand (Eldredge, 1989, 1996, 2003; Miller, 2001, 2002a, 2004; Vrba, 1985, 1993, 2004). How does the plexus of processes—many of which are short-lived compared to those that characterize the bracketing, stable ecological regimes—result in durable regional ecosystems and stable species-lineages able to persist for millions of years with only minimal and generally non-directional changes? An appeal to scaled up local processes probably will not help us much here.

Assembly of New Regional Ecosystems: The Evolutionary Macroecology of Recovery

The fracturing, shrinkage, and separation of population remnants sets the stage for a bout of allopatric speciation, especially if many of the remnants do not collapse to bottlenecks but manage to quickly acquire new adaptive traits. The flurry of new species must include the gamut of speciation products discussed above. Consider just the primary consumers: during a turnover pulse the incumbents either abandon the region, go extinct or speciate. Formerly abundant species could be reduced to extreme rarity, and the previously rare taxa could give rise to abundant descendants. Among the consumers (the pervasive ''arbiters'' of ecosystem structure (Coleman & Hendrix, 2000) and the dominant components of the Phanerozoic fossil record), selection for favored positions in the emerging ecological regime must be extraordinarily stringent, as the new players move simultaneously to dominate or at least secure lucrative places in the emerging regional system. It is possible, however, that many of the new species that have not achieved morphologic differentiation and are not reproductively isolated are also those that fail to detect and secure a stable place in the new economy, with many undergoing species abortion. At the opposite end of the ''success spectrum'', a few of the new players become extremely influential ''hub species'', entraining a constellation of fairly tightly coupled partners—including organisms at other levels in an emerging food web. Such species deploy populations in many of the new local ecosystems and provide habitat structure, insulation from minor disturbances, and food/nutrients for other organisms, either as living biomass, dead tissue, fecal material, or in the form of re-engineered habitats. The retinues of species that discover this kind of resource are assured of economic success as long as the hub species is available. Other species just quickly and effectively master resources or take over real estate, and they do this right from the beginning.

The interaction cells that sweep consumers into stable configurations are a version of what Salthe (1993) referred to as *domains of influence*, and Ulanowicz (1997) characterized as patterns of *system ascendency*. In these views, systems with many potential internal connections settle into more mature configurations, with one dynamic structure emerging (Salthe, 1993: 153). Some of the new species secure lucrative positions immediately; some may be left out in the cold (Ulanowicz, 1997: 53–55). Although the species enthroned as dominant players in the new ecological regime will be deployed in different kinds of local ecosystems, they will perpetually seek their preferred habitats including general position in local economies (Janzen's (1985) notion of *ecological fitting* is a similar idea: all of the key adaptive devices are put in place during emergence of a species, and ecosystems are assembled thereafter without much in the way of pronounced or directional evolutionary modifications). Thus, economic and genealogic entities, all of which are new, imported or resurrected, discover together stable configurations. The species that secure prominent places in the new regional

economy are probably the ones we encounter most often and know the most about, both in neoecological surveys and in the fossil record. The species that do not manage to capture a major slice of the economic pie, or to make a connection to a hub species, may face extinction or amble on as the myriad of rare organisms in the subsequent ecological regime (Miller, 2005).

It is becoming increasingly clear that intrapopulation processes cannot account for species-lineage stability, but that the geographic structure of species having many populations in varied selection regimes provides the most plausible explanation for their staying power (Eldredge et al., 2005). Large ecological systems could be stable because of their ability to recover from disturbance or their ability to persist in the face of environmental change, or by being able to sacrifice some working parts (metapopulations, local systems) and yet continue to have essentially the same organization and function (Miller, 1996), or finally because the component species that provide the populations that make up these ecological systems largely tend to be stable. Although we are just beginning to deal with these problems, we may now have our first glimpse of processes that initiate these patterns of higher-level stability.

Part 3: Pulses of Speciation: How Do New Species Really Rain Down in the Fossil Record?

It is evident from our earlier discussions that there appears to be a distinction between the dynamics of mass extinctions and the more regional events we associate with evolutionary turnover pulses. This distinction is worth exploring in greater detail in light of the difference between the patterns and processes operating when new widespread (or global) evolutionary faunas are founded as opposed to how regional biotas are founded.

Evolutionary Radiation and Rates of Speciation: External Forces Setting the Tone for Diversification

The Cambrian Radiation and the Origins of the Trilobites

The Cambrian radiation represents one of the key episodes in the history of life, marking the geologically rapid transition in the fossil record from few animal species in depauperate communities to diverse species comprising complex communities. The trilobites are among the first undoubted, skeletonized metazoans to appear in the fossil record. They are also the most diverse and abundant Early Cambrian animals. Although it has been suggested that rates of evolution were unusually high during the Cambrian radiation, Lieberman (2001) analyzed rates of speciation in Early Cambrian trilobites and found that although they

were high they did not differ statistically from rates of speciation known for other groups that lived at other times. In short the Cambrian radiation appears comparable to other episodes of dramatic, evolutionary radiation: for instance, the diversification of mammals after the extinction of the dinosaurs. Phylogenetic paleobiogeographic analyses of trilobites conducted by Lieberman (2003b) and Meert and Lieberman (2004) suggested that tectonic events, specifically the breakup of the supercontinent Pannotia at the end of the Proterozoic played an important role in driving the diversification of early trilobite clades. In particular, this major tectonic event may have created numerous opportunities for vicariant speciation.

Middle Devonian Trilobites from Eastern North America

There are several clades of trilobites known from the Middle Devonian of eastern North America; those occurring in strata of the Hamilton Group have been studied in some detail and appear to comprise an important evolutionary radiation. Several of these clades have been subjected to phylogenetic analysis (e.g., Eldredge, 1973; Lieberman, 1994; Lieberman & Kloc, 1997). Further, speciation rates have been quantified in some of these groups (e.g., Lieberman, 1999) and they are significantly lower that those documented in their Early Cambrian kin. A possible explanation for this difference is that the earth history regime prevailing during the Middle Devonian was very different from that of the Early Cambrian. Instead of a supercontinent being split apart, another, Pangea, was in its early stages of assembly. Phylogenetic paleobiogeographic analyses of Middle Devonian trilobites by Lieberman and Eldredge (1996) showed evidence for repeated episodes of geodispersal, followed by vicariance, followed by geodispersal. These appear to be related to repeated episodes of sea-level rise and fall. Such cycles appear to have played an important role in their evolution, whereas specific tectonic events played less of a role (Lieberman, 2005). Further, opportunities for vicariance, at least at the large scale of major continental blocks, may have been more limited in the Devonian relative to the Early Cambrian. This difference may explain the difference in speciation rates in trilobites from these two time periods.

Another important evolutionary radiation of trilobites is known from the roughly coeval Middle Devonian of the Malvinokaffric Province of modern day South America and South Africa (Eldredge & Branisa, 1980; Eldredge & Cracraft, 1980). Although speciation rates have not been considered in detail within these groups, the Malvinokaffric trilobites do show similarities to the Devonian trilobites from eastern North America in their biogeographic patterns. In particular, these seem to show evidence for repeated episodes of geodispersal, followed by vicariance,

followed by geo-dispersal related to cycles of sea-level rise and fall (Lieberman, Edgecombe, & Eldredge, 1991; Lieberman, 1993). The Devonian evolutionary radiations of these trilobites also show intriguing similarities to the diversification of tropical Neogene mammals documented by Vrba (e.g., 1980, 1985, 1992, etc.). In particular, evolutionary and biogeographic patterns in these radiating mammal groups appear to have been profoundly affected by climatic oscillations between cold and warm periods, which caused repeated episodes of vicariance, followed by geodispersal. This radiation were marked by high rates of differentiation (Vrba, 1987), though not as high as those marking the early Cenozoic radiation of mammals.

Thus, one apparent difference between the most dramatic times of evolutionary radiation in the history of life, like the Cambrian radiation or the Cenozoic radiation of mammals, and other times of more modest radiation may center on the prevailing Earth history regime. In particular, the distinction seems to be between times when evolution is governed by major, non-repeating tectonic events, and times when oscillating climatic cycles (or partly related cycles of sea-level rise and fall) are significant. The former mechanisms confer a dramatic increase in the rates of evolution; the latter permit high but not the highest rates of evolution, perhaps because episodes of geodispersal, associated in marine invertebrates with the cycles of sea-level rise or in tropical mammals with climatic amelioration, interrupt or cap the times of vicariant differentiation.

The Initial Stages in the Topology of Evolutionary Radiations

One aspect of the Cambrian radiation of trilobites, and this may be true of other major evolutionary radiations in general, is that there appears to be some hidden evolutionary history. For instance, although trilobites first appear in the fossil record roughly 525–530 million years ago, phylogenetic paleobiogeographic evidence suggests that they had evolved and begun diverging 20–70 million years before their first appearance in the fossil record (Meert & Lieberman, 2004). This hidden history may be the fuse to the Cambrian radiation, although the duration proposed for this fuse is far shorter than some authors had suggested based on older molecular clock studies (e.g., Wray, Levinton, & Shapiro, 1996). In fact, the estimated divergence dates are in line with those from recent molecular clock studies (e.g., Peterson et al., 2004). Lieberman (2003c) argued that this might represent a higher-level analogue to the well-documented phenomenon of punctuated equilibria: new groups appear in narrow and environmentally marginal regions. The result is a displacement between paleontological and evolutionary emergence, with species evolving and persisting for a certain period before

they become abundant enough to be fossilizable. An important point, however, is that the signature of this diversification is preserved in the fossil record.

On smaller scales, a similar phenomenon is visible in the radiation of the Devonian trilobite faunas of eastern North America and parts of the Devonian Calmoniid fauna from South America and South Africa. There, in each case, phylogenetic evidence (for the former see Burton & Eldredge, 1974; Lieberman, 1994; Lieberman & Kloc, 1997; for the latter see Lieberman et al., 1991; Lieberman, 1993) suggests that each evolutionary radiation was already underway for several millions of years before it appeared in the fossil record. The manifest gap is smaller than that associated with the Cambrian radiation, perhaps because a smaller component of phylogenetic and geographic space is involved. In all cases the apparently missing history is on the order of about 10% of the total duration of the group in question: this is similar to the figures invoked in the paradigm examples of punctuated equilibria by Eldredge (1971) and Eldredge and Gould (1972). Further, the notion of missing history is reminiscent of various phylogenetic studies of fossil taxa that considered ghost lineages, including those of Norell and Novacek (1992). Such a value is not insignificant, yet it is not significant enough to make the fossil record an intractable place to conduct evolutionary studies. Our suspicion is that as with punctuated equilibria, except in the exceptional cases where allopatric speciation, or early species flocks, can be witnessed in the fossil record, this is going to be a general feature of the fossil record that merits greater consideration.

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