

LONG-TERM STASIS IN ECOLOGICAL ASSEMBLAGES: Evidence from the Fossil Record*

W.A. DiMichele,¹ A.K. Behrensmeier,¹ T.D. Olszewski,²
C.C. Labandeira,¹ J.M. Pandolfi,³ S.L. Wing,¹ and R. Bobe¹

¹*Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560; email: dimichele.bill@nmnh.si.edu, behrensmeier.kay@nmnh.si.edu, labandeira.conrad@nmnh.si.edu, wing.scott@nmnh.si.edu, bobe.rene@nmnh.si.edu*

²*Department of Geology and Geophysics, Texas A&M University, College Station, Texas 77843; email: tomo@geo.tamu.edu*

³*Center for Marine Studies and Department of Earth Sciences, University of Queensland, St. Lucia, Queensland 4072, Australia; email: j.pandolfi@uq.edu.au*

Key Words ecosystem stability, assembly rules, paleoecology, ecological persistence, environmental tracking

■ **Abstract** Studies of plant and animal assemblages from both the terrestrial and the marine fossil records reveal persistence for extensive periods of geological time, sometimes millions of years. Persistence does not require lack of change or the absence of variation from one occurrence of the assemblage to the next in geological time. It does, however, imply that assemblage composition is bounded and that variation occurs within those bounds. The principal cause for these patterns appears to be species-, and perhaps clade-level, environmental fidelity that results in long-term tracking of physical conditions. Other factors that influence persistent recurrence of assemblages are historical, biogeographic effects, the “law of large numbers,” niche differentiation, and biotic interactions. Much research needs to be done in this area, and greater uniformity is needed in the approaches to studying the problem. However, great potential also exists for enhanced interaction between paleoecology and neoecology in understanding spatiotemporal complexity of ecological dynamics.

INTRODUCTION

The objective of this paper is to review the concept of ecological persistence on the basis of evidence from the fossil record and to evaluate the extent to which such evidence supports the proposition that assemblages of organisms can remain “the

*The U.S. Government has the right to retain a nonexclusive, royalty-free license in and to any copyright covering this paper.

same” over thousands to perhaps millions of years in the face of environmental perturbations and species invasions. Such claims have been made on the basis of data from the marine and terrestrial fossil records, although counterarguments are equally common. In those instances that supposedly document persistence, how has it been measured, and what is indicated about the underlying cause or causes?

Contrasting views of plant and animal communities as ephemeral or persistent entities can be traced back to the works of Clements and Gleason (Golley 1993, McIntosh 1995), which pitted an “organismal” against an “individualistic” model of community organization, respectively. In more recent years, this debate has emerged in other guises. Do communities and ecosystems have emergent properties that might confer some resilience or homeostasis in the face of environmental change? Are they, instead, momentary associations that simply reflect the independent responses of local populations to changing environments and biotic interactions, and is continuity through time thus little more than a happenstance?

The role of the fossil record in our understanding of this issue has focused almost exclusively on Quaternary pollen and spores and to a lesser extent on insects, which have been cited as empirical confirmation of individualism. Here, we bring data from the fossil record, particularly that of the pre-Quaternary, to bear on the questions of long-term stasis in biotic systems. Although conceptual models founded in modern ecology can be difficult to test directly with fossil data, the fossil record may reveal patterns that do not follow from direct extrapolation of neoecological concepts. Finding ways to address empirically the differences in temporal and spatial scales between these sources of data is the challenge that could bring us to a richer and more comprehensive ecological theory.

WHAT DO PALEONTOLOGISTS WANT TO KNOW THAT IS OF RELEVANCE TO ECOLOGISTS?

Paleontologists are interested in the biological, physical, and chemical forces that have shaped evolution, as well as in the phylogenetic and biodiversity-related “what” and the genetic “how” of the history of life. Ecological questions in paleontology involve the role of environment in evolution and focus on many of the same variables that ecologists measure in modern systems (e.g., species richness and other diversity measures, climate, substrate, and biogeography), except that paleontologists and geologists can document these variables, with varying degrees of resolution, over much longer time periods and compare the resulting patterns in different places and through time. Examples of paleoecological questions include:

1. To what degree is the differential diversification of lineages related to environmental or ecological controls as opposed to intrinsic traits, and why have some lineages proliferated and diversified over geological time, whereas others have persisted with little morphological change? This question is

relevant to current ecological issues such as invasive species and draws on a rich geological and fossil record of continental connections, climatic shifts, and successes and failures of lineages over time and in different biogeographic arenas.

2. Why do some assemblages of organisms coexist for long periods of time, whereas other assemblages change rapidly and have little long-term continuity? This question is relevant to current debates about ecological assembly rules and the resilience or interdependency of organisms that co-occur in the same environments.
3. Why are some ancient ecosystems more resistant than others to externally driven biological change (e.g., invasion) or environmental stress (e.g., climate shifts)? The fossil record includes many examples of ecosystem persistence in the face of environmental change and also of thresholds where ecosystems break down and are replaced by novel floral and faunal assemblages.
4. How does ecology affect rates of evolution? Are the effects of species-environment associations on rates of cladogenesis, anagenesis, and extinction discernible? At the time scale of modern ecology, do these questions translate into the effects of environment on ranges and geographic variation of persistently co-occurring taxa, their ability to invade or colonize new habitats, and their susceptibility to habitat change? More simply, could the fossil record provide us with indicators of which species or ecomorphs are more or less resistant to short-term ecological stress or responsive to new opportunities?

ECOLOGICAL VERSUS PALEONTOLOGICAL CONCEPTS AND DATA

Differences in the nature of time, space, and resolution as perceived by ecologists and paleontologists have often led to differences in terminology. Clarification of common ground, while also recognizing irreconcilable differences, is important for future communication. Thus, we begin with a review of basic concepts and terms that also serves to highlight the different domains and perspectives of the ecologist and the paleontologist.

The most evident difference is the scale of time over which change is observed. Ecologists study the response of communities and ecosystems to change on very short time scales, whereas paleoecologists have access to a wide range of temporal scales (Figure 1). Because both migration and speciation occur over time, paleoecologists may borrow, though with caution, some of the descriptive tools developed by ecologists when appropriate for patterns in the fossil record (Miller 1993, 1996; DiMichele 1994). However, a danger of “me-too ecology” exists in which the paleontologist works too hard to serve up paleoecological evidence on a neoecological platter and not only misses important biases in the data but also

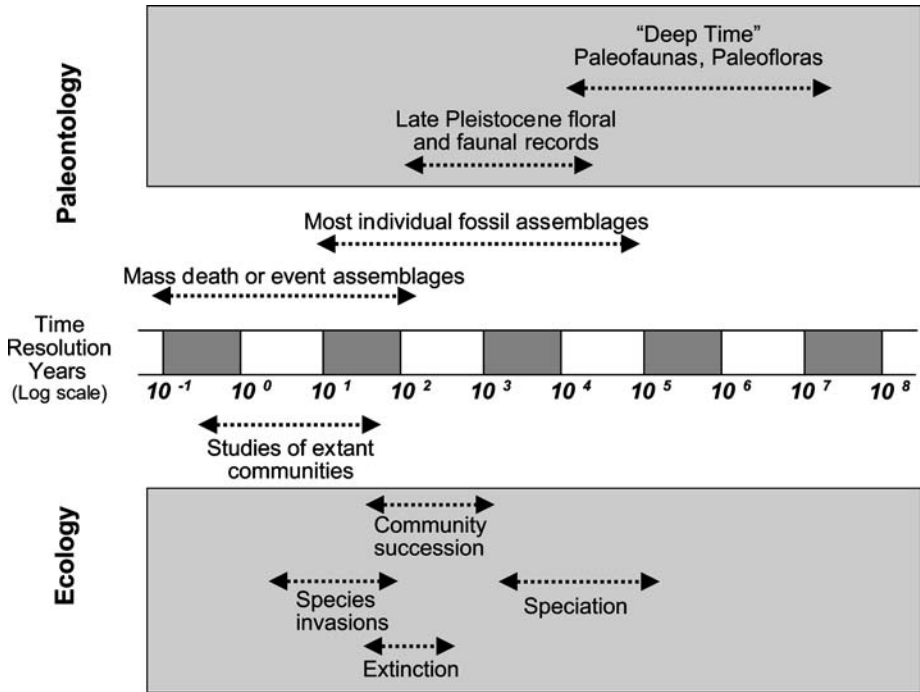


Figure 1 Comparison of the spans of temporal resolution that characterize ecological and paleontological data. Individual fossil assemblages may encapsulate varying degrees of time (i.e., time-averaging), depending on the circumstances of death and burial (taphonomy) and collection method, whereas samples of extant communities generally represent single or repeated censuses over days to decades. In paleontology, long-term floral or faunal records developed from multiple fossil assemblages are the basis for the analysis of paleocommunity stasis or change through time (*upper gray bar*). In ecology, with the exception of speciation, processes that can be observed or inferred in recent ecosystems (*lower gray bar*) occur over much shorter time intervals than can be resolved by paleontological data.

overlooks what might have been truly different about past ecosystems (Olson 1980, 1985).

The basic terms that describe long-term ecosystem behavior have been applied primarily to models in ecology and, thus, are largely conceptual (Pimm 1984). “Complexity” can be determined by the number of species in the system (richness), the number of interspecific interactions (connectance), the magnitude of the interaction among species (interaction strength), and the relative distribution of species abundances in an assemblage (evenness). Pimm (1991) described five ecological meanings for the term “stability.” Each represents a pattern of change through time, independent of time scale and, therefore, applicable to a discussion of paleoecological stasis. Stability of a system is central to ecological stasis. A stable system, when at equilibrium, returns to the equilibrium condition after

perturbation (Holling 1973). A stable system must be understood in terms of a range of variation around some equilibrium point. Related to stability is “persistence,” an empirical measure of how long a system remains unchanged according to some defined measures of its state. “Resilience” is the rate at which a displaced variable returns to its equilibrium value. The shorter the return time, the more resilient a variable or system is. In a different formulation, resilience can be considered a measure of the amount of disturbance a system at equilibrium can absorb before moving to a new stable state (Gunderson et al. 2002). “Resistance” describes the effect on the system of a permanent change in a variable, such as the response to a disturbance. If other variables show little change, then the system is resistant to changes in the altered parameter. “Variability” is the degree to which a parameter varies over time. Although it can be measured with a statistic such as standard deviation, the duration of the examined interval must be noted so that the scale of variation can be accounted for.

The relationship between diversity/complexity and stability remains at the core of debate in ecology (May 1974, Tilman 1999, Cottingham et al. 2001). Topics of contention include the degree to which model systems capture reality, whether the focus of investigations should be on populations or on communities, and the very definition of stability itself (DeWoody et al. 2003). A corollary to these basic concepts is the process of ecosystem assembly and attendant assembly rules (Lockwood et al. 1997, Belyea & Lancaster 1999, Weiher & Keddy 2001), which can be divided broadly into rules of access to a resource and rules of coexistence on that resource.

All these concepts overtly assume that many ecosystems are capable of existing close to an equilibrium point (for a critique, see Peters 1993). They also are consistent with models of hierarchical ecosystem organization, which recognize that emergent properties (properties of the system that are not properties of any of the system’s components, its species) may appear only at certain spatial or temporal scales of analysis (Allen & Hoekstra 1992, Ulanowicz 1997, Maurer 1999).

Systems also can be characterized on the basis of functional types (Simberloff & Dayan 1991, Smith et al. 1997), or ecomorphs, which are groups composed of taxa that are presumed to have similar ecological requirements and to play similar roles within an ecosystem. Systems with high levels of overlap among functional types have high levels of redundancy. High redundancy may be most common in unpredictable and variable environments (Walker 1997), although exceptions certainly abound. Coral reefs, for example, can be considered predictable environments but also can have high species diversity and high degrees of apparent redundancy.

Paleontologists and paleoecologists deal with samples of organisms and environments that are spread out in time as well as in space, and they have developed a system of new terms for unique concepts or different meanings for existing terms that reflect this domain. Fossil species, like living species, are not randomly associated with one another, and this fact allows paleoecologists to recognize biofacies, “a body of rock distinguished on the basis of its fossil content” or “a local assemblage or association of living or fossil organisms, especially one characteristic of some type of marine conditions” (Jackson & Bates 1997). Biofacies can be mapped

through both time and space because different taxa are associated with different environmental conditions. The term has been used primarily in marine deposits where the composition of the biota is constrained by water temperature, depth, energy, turbidity, and chemistry, all of which may be independently recorded in physical and chemical features of the associated sediments. The term has been applied less often to terrestrial deposits, although it is equally useful there, where the flora or fauna is constrained by sedimentary characteristics.

The typical paleoecological sample is an assemblage of fossil remains collected from a single rock layer or stratum or an assemblage combined from individual samples derived from a specified thickness of strata (Behrensmeyer & Hook 1992). In certain cases, such assemblages faithfully represent original ecological communities, for example, a community that experienced a catastrophic death and burial event or one in which all the fossils are composed of rapidly degraded materials such as leaf litter (Wing & DiMichele 1995). In cases of preserved animal hard parts or accumulated resistant plant parts, the sample usually represents a period of time that is long by ecological standards, from 10^2 to 10^5 Kyr (thousands of years) (Figure 1) and, thus, may include organismal remains from more than one ancient assemblage. This incorporation of a temporal element into the sample is referred to as "time-averaging" (Johnson 1960), and is one of the major ways that paleontological faunal and some floral lists differ from ecological ones. Time-averaging also is present in some neoecological studies, such as those that assess plant damage in extant tropical forest litter, which may involve combining data from different seasons, years, or even longer intervals. For fossil assemblages composed of hard parts (e.g., shells, bones, or wood), diversity measures, rank-order of abundance, and other variables are almost always based on samples that combine the results of short-term fluctuations and provide average measures of paleocommunity characteristics over hundreds or thousands of years (Figure 1). This method can be advantageous (Kidwell 2002, Behrensmeyer et al. 2000), but significantly time-averaged paleocommunity data cannot be regarded as strictly comparable to a large proportion of census data for modern ecosystems. Thus, the short-term cycles or trends over the years or decades observed in ecological studies are largely invisible to paleontologists and paleoecologists, especially in the vertebrate or marine invertebrate fossil records. In pre-Quaternary depositional settings, where high temporal resolution can be achieved, correlation of changes in the biota at such a fine scale across a large area ordinarily is not possible. Moreover, the absence of a taxon from a particular assemblage where it might be expected can be the result of preservational sampling biases, collecting methods, or original ecological controls. A number of strategies for coping with such problems are available. These strategies include quantitative assessment of apparent versus real taxonomic ranges (i.e., origination and extinction rates) (Marshall 1997, Foote 2000, Holland 2003), holding depositional context and taphonomic situation constant through time (isotaphonomy) (Behrensmeyer & Hook 1992, Behrensmeyer & Chapman 1993), and modeling time-averaging effects on the basis of modern analogs and "taphonomic control taxa" (Kidwell & Holland 2002).

In both the marine and the nonmarine realms, "paleocommunity" has come to mean a group of taxa that form a recurring, recognizable assemblage of organisms. Criteria for defining the boundaries of biofacies or paleocommunities vary greatly. One of the most stringent definitions is that of Bambach & Bennington (1996), who restricted the term community (i.e., paleocommunity) to groups of collections that cannot be statistically distinguished on the basis of their species composition and abundance. They used the term community type (i.e., paleocommunity type) for aggregates of collections and paleocommunities that have similar but not identical taxonomic composition and occur in similar but not identical environments. This second term acknowledges that significant variation can exist among individual collections because of variation among habitats. In other words, a paleocommunity type (or a biofacies) can represent a metacommunity that varies from place to place on an ecological landscape. Watkins et al. (1973) provided an interesting distinction between Petersen communities, "a local, descriptive unit of recurring combinations of species that can be reproduced in the fossil record," (i.e., a biofacies) and Thorson parallel communities, "groups of Petersen communities related by common ancestry of contained taxa." The second concept explicitly introduces an evolutionary and historical aspect to paleocommunities, which allows them to have continuity through geologic time and global distribution, despite species differences, as long as member taxa represent related evolutionary lineages.

Much has been written about turnover and turnover events or pulses in the land mammal fossil record (e.g., Vrba 1993, McKee 2001). To paleontologists and paleoecologists, turnover means the proportion of extinctions and originations relative to the total number of taxa in a specified time interval. Turnover events are higher than normal rates of turnover relative to a clearly defined "background" rate. In ecology, turnover most typically means a change in species composition over a specified geographic or ecological boundary; that is, turnover in space rather than through time. However, numerous examples exist of turnover occurring over short time scales (years to decades), such as successional changes in old fields or after tree fall in forests, or after storms in marine systems. These uses of the term turnover touch on the much larger issue of the validity of using ecological variability on a modern time scale as an analog for temporal variability and change through the geological record.

As in studies of modern ecosystems, functional types, or ecomorphs, have also been examined in the fossil record in an attempt to reduce the effects of phylogenetic history and focus on patterns of stability or change in suites of functionally related characters. Examples include both whole communities and specific ecological features of fossil mammals (Damuth 1992, Van Valkenburgh 1995, Janis et al. 2000), plants (Wing & DiMichele 1992, DiMichele et al. 2001b), and insects (Labandeira 1998, 2002).

Application of Watkins et al.'s (1973) concept and related concepts that incorporate a historical dimension to communities has led to research in the global paleobiogeography and evolutionary history of diverse paleocommunities (Boucot 1975, Boucot & Lawson 1999). On the basis of this work, Boucot (1983) defined a

series of Ecologic-Evolutionary Units (EEUs) in the Phanerozoic and emphasized the ecological context of evolution within this framework. Other workers, however, following Gleasonian traditions, maintain that paleocommunities are simply associations of taxa with similar habitat preferences and do not represent an emergent level of biotic organization (Hoffman 1979, Jablonski & Sepkoski 1996). Resolving this dispute remains an important focus in evolutionary paleobiology.

ARE PERSISTENT COMMUNITY ASSEMBLAGES POSSIBLE?

At least four hypotheses have been proposed to explain the persistence of community composition over geological time. First, species co-occurrence may reflect evolved ecological relationships that confer net mutual benefits when species occupy the same environment at the same time. Such species interactions may determine community structure and function (e.g., competition, symbiosis, or predation). Second, a significant overlap in species environmental tolerances may exist such that some species almost always occupy the same environment. Third, geographic isolation may occur because of such factors as place of evolutionary origin, vicariance patterns, and natural geographic barriers; these factors, previously set in motion, may be responsible for species co-occurrence at any given time. Fourth, the “law of large numbers” may apply, which states that the most abundant species remain most abundant because they tend to produce more offspring than the less abundant species.

Individualistic Versus Interactive Models

Central to ecological stasis is the nature of the organization of ecological assemblages. Are communities simply short-term associations of species living together because of momentarily similar responses to environmental conditions (Gleason 1926), or are such assemblages integrated in some manner that leads to emergent, system-level properties (Clements 1916)? This discussion dates to the early twentieth century (Golley 1993) but continues today in debates over assembly rules (Belyea & Lancaster 1999, Weiher & Keddy 2001), the effects of biodiversity on ecosystem stability and productivity (May 1974, Cottingham et al. 2001), and the proper construction of null models (Gotelli & Graves 1996, Hubbell 2001).

Until now, the paleontological studies that have been most widely recognized by neoecology are those that have offered support to the proposition that “communities” are transient associations of species that share similar resource requirements under a given set of climatic/environmental conditions. Most of this evidence came initially from palynological studies of the last interglacial interval in the Northern Hemisphere temperate zone (Davis 1986, Webb 1987). More recently, the records of terrestrial vertebrates (Graham 1997) and marine invertebrates (Jablonski & Sepkoski 1996, Patzkowsky & Holland 1999) have been used to document the

same position, but examples to the contrary have also been presented (Pandolfi 1996, 2000). The nature of this individualism is not universally agreed upon, however, and may be dependent on scale of analysis; it may be most evident at some smaller scales within environmentally bounded species pools (biomes in the terrestrial world) but not at larger scales between species pools, where species exchange is less common.

Patterns of Stratigraphic Persistence

Olson (1952, 1958, 1980) was among the first paleontologists to document community persistence through well-defined intervals of rock strata by presenting case studies from the Permian deposits of Texas and Oklahoma. Olson established the term *chronofauna* for such assemblages of vertebrate taxa that recurred through long stratigraphic intervals and attempted to reconstruct food webs for the component species (Olson 1952). Numerous examples of fossil vertebrate faunas reflect some degree of continuity through time, although whether these faunas could be considered communities in the ecological sense is debatable. North American Cenozoic "Land Mammal Ages" and their equivalents on other continents are based on the persistence of suites of taxa for particular chronostratigraphic intervals, which allows correlation over wide geographic areas (Woodburne 1987, Janis et al. 1998). At a rather coarse level of resolution, the success of such schemes attests to the persistence of at least some components of mammalian faunas and the communities of which they were a part. Basically, the pattern at both regional and continental scales is similar to that observed in the marine invertebrate and plant fossil records; long intervals of relative stability are punctuated by periods of rapid change.

A similar pattern of assemblage persistence has been described by Boucot (1978, 1983) in the course of carrying out biostratigraphic and evolutionary studies of marine faunas. He recognized that invertebrate assemblages did not demonstrate patterns of continuous turnover but rather were organized into temporally coherent units between which significant differences existed (EEUs) and within which smaller units, or communities, could be recognized on the basis of recurrent patterns of composition (Sheehan 1996).

Brett & Baird (1995) introduced the term *coordinated stasis* to connote a pattern of bimodal evolutionary turnover within benthic marine biofacies of the Silurian and Devonian of the Appalachian Basin (Table 2). They reported a pattern in which the majority of species within a biofacies showed little, if any, evolutionary change over a period of several million years (Myr), followed by rapid extinction and replacement of those species in the same environment. To provide explicit criteria for comparison with other time periods and geographic areas, Brett et al. (1996) stated that coordinated stasis units should exceed 1 Myr in duration, during which approximately 60% of species should persist and show little morphological change. In this scheme, fewer than 40% (typically fewer than 20%) of species cross the bounding intervals, which should be no more than one tenth of the

duration of the static intervals. Speciation and extinction are concentrated in the intervals of rapid turnover. The pattern of coordinated stasis need not imply strong Clementsian codependence within a community. Episodic environmental change could affect many evolutionary lineages that act independently of one another. In such a case, a pattern of coordinated stasis would reflect the timing and severity of punctuated environmental changes. Additionally, samples from a coordinated stasis unit need not all display identical species composition or abundance; room for environmental variability exists within a biofacies, as acknowledged in the definition of Bennington & Bambach's (1996) paleocommunity types (similarly by Olson 1952, 1985). Rather, the pattern is defined by coincident turnover that punctuates protracted periods of community-wide morphological stasis. Although the pattern of coordinated stasis could simply result from episodic environmental change, some authors have interpreted it as reflecting the influence of ecological interactions on the evolutionary trajectory of the lineages within a community. Morris et al. (1995) suggested a mechanism of ecological locking, "a mechanism by which ecological interactions prevent evolutionary change, resulting in long-lasting, stable systems capable of resisting some types of disturbance" (Morris et al. 1995, p. 11,272), as the necessary implication of coordinated stasis in the fossil record. Whether or not ecological locking is correct, it is not the only possible explanation of the pattern of coordinated stasis.

Coordinated stasis has been challenged because of the supposed implications of strong species interactions as a cause of the pattern (e.g., Buzas & Culver 1994, Patzkowsky & Holland 1999). In addition, strong arguments have been made regarding the need for statistical analysis of supposed patterns of persistence (Bennington & Bambach 1996, Bambach & Bennington 1996); that is, just how much variation can occur if assemblages are to be considered the same through time? Alroy (1996) carried out a statistical analysis of an extensive compilation of mammalian stratigraphic ranges and determined that the expectations of the coordinated stasis model, such as pulse-like turnover of species, did not hold.

Is the "Unified Neutral Theory of Biodiversity and Biogeography" a Link Between Rates of Taxonomic Change and Community Structure?

One of the difficulties of studying community stability in the fossil record is that most ecological models of community structure implicitly assume a static equilibrium for species richness and abundances (see review by Tokeshi 1993). An alternative approach that has received much recent attention is neutral modeling of community dynamics. Hubbell's (2001) *The Unified Neutral Theory of Biodiversity and Biogeography* assumes that local communities maintain a constant number of individuals. Consequently, new individuals can only enter the community by filling vacancies opened by the death of established individuals. Three mechanisms of replacement exist in Hubbell's model. First, a death can be offset by the birth to a parent already present in the local community. Second, an individual

from the surrounding metacommunity can be recruited to fill the vacant slot and can represent a species that is not already a member of the local community. Third, a local birth could also be a speciation event, so the replacement individual represents an entirely new species. This system is neutral because all individuals have an equal probability of dying, reproducing, and speciating in a given time interval, regardless of their species identity.

The model predicts an equilibrium abundance distribution and expected richness, given the size of the community, the degree of exchange with the surrounding metacommunity, and the rate of per capita speciation (incorporated into Hubbell's fundamental biodiversity number). In contrast to statistical or niche-partitioning models (Tokeshi 1993), Hubbell's model predicts change in the taxonomic composition through time because of community drift, which reflects the constant stochastic elimination and replacement of individuals. Although common species are expected to endure longer than rare species, a consequence of large numbers effects, newborn species (or previously rare species colonizing new habitat) are not likely to rise to dominance, and previously dominant species are not likely to go extinct. The rate and likelihood of these events depends on the model parameters.

The potential usefulness of a neutral modeling approach for paleoecology lies not in whether it is right or wrong, but rather that it provides a first step toward developing a theory that ties evolutionary history to the structure of ecological communities and focuses on aspects that can be measured by use of fossil data (i.e., rates of origination and abundance distributions). Time will tell whether this potential will be fulfilled (Chave 2004), but some paleontological tests have already been formulated (Pandolfi 1996, Pandolfi & Jackson 1997, Clark & McLachlan 2003, Olszewski & Erwin 2004).

CASE STUDIES: TERRESTRIAL RECORD

The case studies mentioned in this section are summarized in Table 1.

Palynofloras: Compositional Stasis and Temporal Scale of Observation

Stasis in the composition of biotas has been observed over a wide variety of spatial and temporal scales, but many of the observations that suggest rapid and unpredictable change in community composition were derived from the past 40 Kyr of Earth history—the time during which samples can be dated by radiocarbon methods. An important question, particularly in considering the relevance of paleontological data for ecological theory, is whether changes in the temporal scale of sampling affect the detection of stasis.

To test whether temporal scale has an effect on detecting stasis in composition, we downloaded fossil pollen data from the World Data Center for Paleoclimatology (WDCP) (<http://www.ngdc.noaa.gov/paleo/pollen.html>). Each dataset consisted of counts of the abundances of pollen taxa in core samples. Abundance data are

TABLE 1 Summary of paleontological studies with evidence relating to persistence and punctuated change in terrestrial paleocommunities of vertebrates, invertebrates, and plants^a

Authors	Study (age)	Duration	Resolution	Geographic scale	Taxa	Patterns through time
Barry et al. 1995, 2002	Siwalik mammals, Middle to Upper Miocene (10.7–5.7 Mya)	5 Myr	100 Kyr	Potwar Plateau, northern Pakistan	115 mammal taxa: Insectivora, Scandentia, Primates, Tubulidentata, Proboscidea, Lagomorpha, Perissodactyla, Artiodactyla, Rodentia Pholidota	Background turnover relatively high (50%–60%) but not correlated with changes in fluvial paleoenvironments; three turnover events within 100–300 Kyr intervals account for 44% of the faunal change; extinctions and appearances are not coincident in time, latter two of the three turnover events appear to be correlated with climate change
Bobé et al. 2002	Omo Shungura Formation (4.0–1.5 Mya)	2.5 Myr	3–100 Kyr	Southern Ethiopia, northern Turkana Basin	Mammals: bovids, suids, primates	Persistence of most taxa with species turnover at 2.8 Mya and after 2.0 Mya; dominant bovids stable from 3.5 to 2.0 Mya, new dominants subsequently; large mammal paleocommunity as a whole stable for 300 Kyr interval followed by 100 Kyr cyclicity in taxonomic abundances
DiMichele & Phillips 1996b, DiMichele et al. 1996, 2002	Pennsylvanian (Desmoinesian/Westphalian D, 306–310 Mya and Missourian/Stephanian A 303–306 Mya)	4 plus 3 Myr	Coal beds and assemblages within a coal bed: 1–10 Kyr	Southern Illinois Basin	Peat-forming plants preserved in coal balls; lycopsids, ferns, sphenopsids, pteridosperms, cordaites	Recurrent intraswamp community patterns among successive coal beds during the Westphalian; patterns terminated by a major extinction at end of Westphalian; replacement of the Desmoinesian communities by new kinds of persistent assemblages in the Missourian

DiMichele & Aronson 1992	Pennsylvanian and Early Permian	17.5 Myr	Fossiliferous clastic beds: 100 yr–1 Kyr	Europe and North America	Plants: compression floras	Two distinct biomes/species pools that persist side by side in the tropics through the Pennsylvanian and into the Early Permian with few common species (mainly weedy wetland forms)
Labandeira et al. 2002	Latest Cretaceous and earliest Paleocene (~66–64 Mya)	2.2 Myr	20 Kyr	Williston Basin, North Dakota, North America	Insect damage: 51 types documented on > 13,000 dicotyledonous leaf fossils	Insect damage diverse and persistent before the Cretaceous-Paleocene boundary, then damage levels and diversity decrease particularly for host-specialist insects; this pattern persists through 800 Kyr of the early Paleocene
Wilf et al. 2001	Latest Paleocene to early middle Eocene (~56–43 Mya)	13 Myr	Individual samples probably represent <1 Kyr	Green River and Uinta basins, North America	Insect damage: 40 types documented on 2435 leaf fossils from 58 host species	Three sample levels based on six quarry sites across the Eocene Continental Thermal Maximum (ECTM) interval show persistence in feeding types but changes in intensity and distribution of damage based on host-plant ant herbivore strategies
Olson 1952, 1958	Early Permian (Clear Fork Group) (~275 Mya)	3–5 Myr	Individual assemblages probably represent 100s to 1000s of years	North central Texas, North America	21 genera and 32 species: fish, amphibians, reptiles	Faunal assemblages associated with different environments (upland, stream, pond margin, and pond) can be followed through time and persist during periods of environmental change with some turnover but overall continuity in the taxonomic and ecomorphic character of the chronofauna

(Continued)

TABLE 1 (Continued)

Authors	Study (age)	Duration	Resolution	Geographic scale	Taxa	Patterns through time
Scott 1978	Late Carboniferous (Westphalian B, 311–313 Mya)	3 Myr	Fossiliferous clastic beds: 100 yr–1 Kyr	West Yorkshire coal measures, United Kingdom	Plants: compression floras	Recurrent paleoenvironmentally specific plant assemblages identified from multiple sampling horizons through time; links lithological patterns to biological patterns and shows they are recurrent (biofacies)
Pfefferkorn et al. 2000	Lower Carboniferous (Namurian A, 320–327 Mya)	6.2 Myr	Fossiliferous clastic beds: 100 yr–1 Kyr	Ostrava-Karvina Basin, Czech Republic	Plants: compression floras	Recurrent plant associations recognized for periods of about 2 Myr each, punctuated by a rapid turnover and establishment of new types of species assemblages in next interval of persistence
Pfefferkorn & Thomson 1982	Late Carboniferous (300–319 Mya)	19 Myr	Fossiliferous clastic beds: 100 yr–1 Kyr	Europe and North America	Plants: compression floras	Analysis at major group level (orders); recurrent associations of taxa and environments of deposition (biofacies) with a major change in dominance patterns occurring near the Westphalian-Stephanian boundary (paralleling coal-ball patterns)
Falcon-Lang 2003	Late Carboniferous (Westphalian A, 313–315 Mya)	1.6 Myr maximum	Fossiliferous clastic sedimentary cycles, 50–200 Kyr duration with finer resolution of individual beds	Joggins Formation, Bay of Fundy, Nova Scotia	Plants: compression floras	Eight transgressive-regressive sedimentary cycles, glacially driven; three recurrent plant assemblages: wetland, dominated by lycopsids; dryland, dominated by cordates and sigillarian lycopsids; and coastal, dominated by progymnosperms and gymnosperms

^aAbbreviations: Mya = millions of years ago; Myr = millions of years; Kyr = thousands of years.

desirable because over geologically short time periods, local extinction or immigration of species is rare. We also used pollen data from the Paleogene (Wing & Harrington 2001).

Change in the composition of the pollen assemblages through time was quantified by application of squared chord distance (Cd_{ij}), a dissimilarity measure that incorporates relative abundance data (Overpeck et al. 1985). Time-steps between samples (t) were calculated from age models in the WDCP pollen database (Quaternary data), or from magnetostratigraphic, biostratigraphic, and isotopic correlation to the Global Magnetic Polarity Time Scale (Paleogene data). Ages of samples between dated horizons were interpolated.

If community composition were completely static, Cd_{ij} would equal 0 between any pair of samples. In the real world, fluctuations in sample composition result from small changes in assemblage composition (e.g., tree falls or local fires) or from small changes in the way the vegetation is represented by the pollen sample. If these small, unpredictable fluctuations in composition are not directional, no correlation should exist between the Cd_{ij} and the time difference (t) between samples i and j . If change in floral composition is directional, a significant positive correlation should exist between Cd_{ij} and t .

The analysis of both Quaternary and Paleogene assemblages reveals that large changes in composition are rare, and most change in composition is fluctuating; therefore, Cd_{ij} is poorly correlated with t . Consequently, samples of similar age give high rates of compositional change (Cd_{ij}/t is large because t is small), whereas samples separated by more time yield low rates (Cd_{ij}/t is small because t is large). Rates of change in floral composition are, thus, highly inversely correlated with t , and rates measured over different intervals are difficult to compare. Short-term (e.g., less than 10 Kyr) fluctuations in composition are likely missed in deep-time datasets, which would, thus, appear to be stable. Conversely, Quaternary datasets generally are too short to capture rare extinctions or immigrations; thus, they do not show the irreversible changes in species-pool composition that are seen in many deep-time records. Differing temporal resolution thus complicates the comparison of rates of change.

Carboniferous Wetland Assemblages

The Late Carboniferous (Pennsylvanian) was a time of generally cool global climate with intervals of intense tropical precipitation that supported rainforests (Gastaldo et al. 1996) and vast peat swamps that became the coal beds of Europe and the eastern United States. Upper Carboniferous rocks appear to reflect, in part, glacial periodicity and may preserve Milankovitch cyclicity (Algeo & Wilkinson 1987). Fossil remains of the plants from peat swamp (mire) forests are preserved as “coal balls” (petrified peat), as compression-impression fossils in mudstones and sandstones, or as spores and pollen. The occurrence of plant fossils in multiple coal beds and in the intervening rocks permits the study of changes in plant composition through time under recurrent, common environmental conditions

(isotaphonomy, *sensu* Behrensmeyer & Hook 1992). Within coal beds, fossil plant and spore-pollen samples can be collected incrementally, which permits vegetational dynamics to be resolved at time scales of less than 100 Kyr. In addition, dynamics can be examined at many sampling horizons (i.e., coal beds) and, thus, through multiple glacial-interglacial cycles and in response to both background and large-scale extinctions (Phillips et al. 1985).

Phillips and coworkers (DiMichele & Phillips 1996a,b; DiMichele et al. 1996; DiMichele et al. 2002) examined more than 50 coal beds, which represented more than 10 Myr, and reported the following basic patterns. Within any one coal bed, multiple, recurrent plant communities can be identified statistically. These communities recur in successive coals, recognized by the approximate rank-order of abundance of the dominant elements; minor taxa vary widely in abundance. A major extinction eliminated nearly two thirds of the species at the Middle–Late Pennsylvanian boundary, approximately 306 million years ago (Mya). This extinction appears to have been caused by a short pulse of global warming and drying in the tropics (Phillips & Peppers 1984, Frakes et al. 1992). After a brief interval of high variability in dominance patterns immediately after the extinction (Peppers 1996), peat-forming landscapes reorganized, and groups previously in low abundances, particularly opportunistic tree ferns, rose to dominance by replacing the prior dominants that had been eliminated by the climatic changes. This represented an internal reorganization of the ever-wet peat-substrate species pool. The pattern of vegetational persistence has been detected in Late Pennsylvanian peat-forming environments (Willard et al. 2004) by an analysis of rank-order distribution of dominant tree ferns in several successive coals in eastern Illinois. A parallel change in dominance patterns in tropical floodbasin floras occurred at approximately the same time, although the reported taxonomic resolution is at the level of families and classes (Pfefferkorn & Thomson 1982).

Patterns similar to those found in coals have been documented in floras from floodbasin sedimentary rocks (sandstones and mudstones) lying between coal beds. In deep-core samples from the beginning of the Late Carboniferous ice age taken from the Ostrava-Karvina coal basin in the Czech Republic, three to four vegetational units that conform to distinct sequential rock formations, separated by abrupt compositional turnover, were identified statistically (Pfefferkorn et al. 2000). In Westphalian B age clastic rocks from England, Scott (1978) identified recurrent patterns of species association with particular sedimentary environments (biofacies) over a 3-Myr time interval. Specific, recurrent sedimentary environments have been tied to qualitatively identified plant assemblages of distinctively different dominance and diversity patterns in the well-known Joggins section in Nova Scotia (Falcon-Lang 2003). The temporal patterns of vegetational change have been placed in a sequence-stratigraphic framework, in which rock units have been related to cycles of rising and falling sea level, presumably controlled in large part by cycles of glaciation and eustasy.

In the north temperate Angaran floristic province, Meyen (1982) documented an extensive stratigraphic sequence of Carboniferous floras at the species level. Assemblage membership persists in this stratigraphic sequence over many sampling

units (beds) though time. Floristic changes occur essentially instantaneously between longer intervals of persistence.

Biome Exchange Patterns in the Late Paleozoic Tropics

During the Late Pennsylvanian and Early Permian, floras dominated by phylogenetically advanced, xeromorphic seed plants began to appear in the tropics. The fossil record shows these new plants intercalated between wetland floras in association with indicators of seasonally dry climatic conditions (Cridland & Morris 1963, Mamay & Mapes 1992, Rothwell & Mapes 1988). Ziegler (1990) referred to this biome as “summer wet.” The seasonally dry/summer-wet biome and its flora ultimately replaced the ever-wet biome in the tropics as global glaciation ended in the Early Permian (see papers in Martini 1997). Broutin et al. (1990) and DiMichele & Aronson (1992) demonstrated that little floristic mixing occurred between these two species pools. Fragmentary evidence of the seasonally dry biome, in the form of transported conifer scraps, appears millions of years before the first in situ macrofossils (Lyons & Darrah 1989), which suggests growth in remote, well-drained upland areas. A biome characteristic of yet drier conditions, composed of still more phylogenetically derived plants, characteristic of the Late Permian and Mesozoic, appeared in the Early Permian in association with gypsum beds (DiMichele et al. 2001a). This unusual and unexpected flora reiterates the earlier pattern of precocious conifer occurrence and again implies strong ties of different biomes or vegetation types to different climatic-edaphic conditions.

These examples demonstrate that when similar environmental conditions can be identified over long intervals of time (in effect, removing significant environmental variation as a causative factor), species-pool composition may persist, and quantitative relationships among these species also may recur. This observation does not mean that similar environments caused the persistence. In fact, neither the persistence of species dominance-diversity patterns nor sharply defined, long-lasting boundaries between species pools are general expectations under the tenets of species individualism, given the continuously occurring effects of disturbance, migration, and low-level environmental variation.

Stability Within Versus Between Trophic-Level Interactions: Fossil Insect Patterns

Typically, most paleoecological data are collected within a trophic level, a taxonomic group, or both, such as analyses of Paleozoic corals, Mesozoic ammonites, or Cenozoic plants. Intertrophic data and comparisons usually focus on taxon-specific ecological interactions that have a relatively good and persistent fossil record, such as Paleozoic platyceratid gastropods and their crinoid and blastoid associates (Baumiller & Gahn 2002) or Cenozoic naticid gastropods and their molluscan prey (Kelley & Hansen 2001). Insect-feeding traces on fossil leaves provide evidence for the broadest effects of one trophic level on another in terms of diversity, abundance, and persistence of associations and in their implications

for community-level ecological reorganization. A broad spectrum of insect damage has been documented on various plant organs, especially leaves, throughout the post-Silurian terrestrial record (Labandeira 2002).

Two case studies are relevant to establishing intertrophic inferences: the sudden end-Cretaceous extinction event, and the Early Cenozoic Thermal Maximum (ECTM) (Table 1). The Cretaceous-Paleogene and ECTM studies detect sudden to prolonged intervals of persistent insect damage patterns as well as wholesale shifts in community-wide structure that involved a cascade of floral changes that had significant impact on feeding patterns of constituent insect herbivores.

Fossil floras from the late Cretaceous and early Paleogene provide an excellent record of insect damage in lieu of a poor record of insect body fossils (Labandeira et al. 2002). In the geographically extensive Williston Basin of North Dakota, 143 floras from 106 time slices encompass a 2.2-Myr interval that straddles 183 m of the Cretaceous-Paleogene boundary (Table 1). The average geochronologic resolution is 20 Kyr, although the stratigraphic placement of samples throughout the section is not uniform. Patterns of insect herbivory were diverse and persistent before the boundary. This abundance was followed by a significant decrease in the diversity and level of insect herbivore damage at the Cretaceous-Paleogene boundary. Host-specialist insects suffered preferentially greater extinction at the boundary than generalists. Finally, no post-event rebound is evident within the 0.8-Myr interval of the earliest Paleocene, although other data (Wilf et al. 2001) indicate return several Myr later.

A profound change in the physical global environment occurred from the latest Paleocene through early-middle Eocene (Zachos et al. 2001), described as the ECTM, mentioned above. A study in which floras from the Greater Green River and Uinta Basins of the Western Interior were used (Wilf et al. 2001) documented insect herbivory from the beginning of the ECTM (56 Mya; humid warm-temperate to subtropical climate, predominantly deciduous plants) to near the maximum (53 Mya; humid subtropical climate, mixed deciduous and evergreen plants) and significantly after the peak warming (43 Mya; seasonally dry subtropical climate, mixed deciduous and thick-leaved evergreen plants). Throughout the entire 13-Myr interval, significantly more herbivory occurred on plant hosts with shorter-lived and thinner leaves than on plants with longer-lived and thicker leaves. This variance in herbivore modes was statistically separable throughout the three time slices examined and widened during the middle Eocene. These data, consistent with modern herbivore defense theory (Coley & Barone 1996), demonstrate that during these major climatic shifts, herbivory was partitioned into an accommodationist strategy that allowed for high levels on deciduous mesic hosts and an antiherbivore defensive strategy of lower levels on strongly defended, mostly evergreen plants.

These studies represent two very different modes of community-level reorganization among insects and their plant hosts. The Cretaceous-Paleogene boundary study indicates a major disruption of associational diversity that took until the Paleocene-Eocene boundary to return to predisturbance levels. As for the latest ECTM, no significant loss of insect feeding types within floras or local community-wide rearrangement of insect-plant associations occurred, but significant changes

did occur in intensity and distribution of damage based on highly defended versus poorly defended plant antiherbivore strategies.

Turnover in Miocene Mammalian Faunas of Pakistan

More than 3 decades of work on the vertebrate faunas of northern Pakistan has generated a 10-Myr record of stasis and change in the mammalian community of this region and allows a comprehensive examination of evolutionary and ecological change in relation to environmental parameters (Barry et al. 2002). The intensively sampled Siwalik deposits (more than 40,000 fossil specimens) provide a temporal resolution of 100 Kyr between 10.7 and 5.7 Mya, which Barry et al. (2002) suggest may be the finest feasible level of resolution for long sequences of vertebrate-bearing strata. By use of a large suite of 115 mammal taxa, Barry et al. (2002) demonstrated a moderately high and persistent level of "background" turnover (50% to 60%) over a period of 5 Myr. Superimposed on this background are three separate short-term turnover events that also changed the character of the mammalian community. The first event involves extinction of many long-lived taxa that are recorded in southern Asia before their demise 10.3 Mya. The second and third events are separated by only about 500 Kyr and occur at 7.8 and between 7.3 and 7.0 Mya during a time of independently documented climate change toward intensified monsoons and the spread of grassland habitats (Dettman et al. 2000). Barry et al. (2002) concluded that this study supports neither the notion of coordinated stasis nor environmentally driven turnover events as the dominant mode of faunal change through time. However, turnover events documented in the Siwalik record have 3 to 13 times the expected rate relative to the background turnover (background average of 1.5 taxonomic appearances or disappearances per 100 Kyr compared with 9, 5, and 20 times the expected rate during the three turnover events). This finding provides evidence for some degree of stability of faunas in the Siwalik ecosystem over time intervals that were very long relative to modern communities. Reinforcing this notion is the fact that major changes through time in the Siwalik fluvial systems had no apparent impact on the composition of the fauna; that is, no correlation of lithologic or paleoenvironmental change with the turnover events occurred. This observation indicates that the mammalian fauna, in successive time-averaged samples of approximately 100 Kyr each, was resistant to changes in the substrate environment but sensitive to the major climate changes of the late Miocene.

Stability and Change in the East African Pliocene Mammal Record

The African late Cenozoic fossil record has been subject to intensive research because of interest in human evolution, and this research provides some of the highest resolution paleontological evidence available for mammalian community structure through time. Deposits along the lower Omo Valley in southern Ethiopia include a sequence of nearly 800 m of sediments from approximately 4 to 1 Mya (Brown 1994, de Heinzelin 1983, Feibel et al. 1989). A large and carefully

documented collection of more than 40,000 fossil specimens from the Shungura Formation provides examples of faunal change at a number of different temporal scales (Bobe et al. 2003, and references therein). Analysis for ecological patterns has been done for specific groups of mammals (bovids, suids, and hominins and other primates), and time intervals can be resolved to approximately 10^3 years in parts of the sequence (de Heinzelin 1983).

The time encompassed by the Shungura Formation coincided with major climatic and environmental changes in Africa (deMenocal 1995, Vrba 1995), and some of these changes are correlated in time with changes in the mammalian fauna (Alemseged 2003, Bobe et al. 2002, Bobe & Eck 2001). Species turnover, based on first and last occurrences, is low overall between 3.5 and 2.0 Mya; the only marked turnover event occurred at 2.85 Mya and corresponds to the onset of Northern Hemisphere cooling (deMenocal & Bloemendal 1995). Examination of the relative abundances of the major mammalian taxa (4,820 specimens) provides a higher resolution record of faunal change in which a period of stability between 2.8 and 2.5 Mya (five stratigraphic sample levels) is followed by a cyclical pattern of shifting taxonomic dominance over 100-Kyr intervals up to 2.0 Mya (Bobe et al. 2002). Statistical tests indicate that the interval of stasis is unlikely to be sampling error, which provides evidence for ecological stability over several hundred thousand years, when global climates were becoming cooler and more variable (deMenocal & Bloemendal 1995). Bobe et al. (2002) speculate that the paleo-Omo River system, with its large drainage area, helped to buffer the lower riverine floodplain and gallery forest habitats from the impact of larger-scale climate change. This effect persisted for several hundred thousand years, until around 2.5 Mya, when external changes finally penetrated the local system and destabilized the ecological communities of the lower Omo Valley.

The Shungura sequence provides additional evidence for faunal stability and ecological persistence. The two most abundant species of the dominant family (Bovidae) co-occur throughout the interval from about 3.5 Mya to 2.0 Mya, with *Aepyceros shungurae* (early impala) and *Tragelaphus nakuae* (similar to bongo) alternating in first and second place (Bobe & Eck 2001). This persistent association may indicate that both species had similar tolerance limits for the wooded and moist environments of the Pliocene-Pleistocene lower Omo River. After 2.0 Mya, during a period of increased environmental change, *T. nakuae* became extinct, and *A. shungurae* became a less conspicuous element of the Omo bovid fauna.

CASE STUDIES: MARINE RECORD

The case studies mentioned in this section are summarized in Table 2.

Soft-Bottom Benthic Invertebrate Faunas

Studies of turnover through time in pre-Quaternary, marine, soft-bottom communities can be somewhat arbitrarily divided into two categories on the basis of their

TABLE 2 Examples of long-duration and high-resolution paleontological studies, with evidence relating to persistence and punctuated change in soft-bottom paleocommunities of marine invertebrates^a

Authors	Study (age)	Duration	Resolution	Geographic scale	Taxa	Patterns through time
Long-Duration Studies						
Ludvigsen & Westrop 1983, Westrop 1996, Westrop & Cuggy 1999	Upper Cambrian (Marjuman-Sunwaptan Stages) ~495–500 Mya	10–15 Myr	~1 Myr biozones	North American continent	Trilobites: >50 supraspecific taxa	Generic-level stability punctuated by three large extinction events; generic composition persistent within intervals between extinctions; species exhibit continuous turnover; each extinction followed by rapid radiation; turnover episodes cut across biofacies; inarticulate brachiopods have longer species longevities (i.e., greater persistence) than trilobites
Patzkowsky & Holland 1997	Upper Ordovician (Mohawkian and Cincinnati Series) ~455–480 Mya	17 Myr	Depositional sequences ~1.3 Myr each	Eastern North America	Articulate brachiopods: 96 genera, 441 species	Three periods of low turnover separated by two episodes of rapid turnover; earlier turnover episode reflects elevated extinction rates and later episode reflects invasion of new genera; turnover events correspond to extreme perturbations of regional ocean-climate system
Brett & Baird 1995	Silurian and Devonian (Llandovery through Givetian Series)	45 Myr	Evolutionary-ecological subunits 2–8 Myr each	Appalachian Basin in New York State	Corals, bryozoans, brachiopods, mollusks, trilobites, echinoderms, and other groups (hundreds of species)	Very high persistence within ecological-evolutionary subunits punctuated by episodes of very rapid turnover; extinction events closely followed by rapid radiations; nearshore assemblages show greater taxonomic persistence than open-marine assemblages

(Continued)

TABLE 2 (Continued)

Authors	Study (age)	Duration	Resolution	Geographic scale	Taxa	Patterns through time
Olszewski & Patzkowsky 2001	Pennsylvanian-Permian (Desmoinesian to Wolfcampian Series) ~280–310 Mya	17.5 Myr	450 Kyr cyclothem	Northern midcontinent in Kansas and Nebraska	Brachiopods: 38 genera, 102 species; bivalves: 47 genera, 94 species	Low but constant rates of background turnover punctuated by episodes of appearance or disappearance; appearance and disappearance episodes not correlated in time; turnover histories of brachiopods and bivalves not correlated
Tang & Botjter 1996	Jurassic 142–206 Mya	28 Myr	Depositional units 2 to 6 Myr	Western North America	Bivalves: 49 genera, 79 species	Episodes of elevated turnover could not be recognized; high levels of species persistence reported; origination and extinction of taxa in this region not closely correlated in time
High-Resolution Studies						
Holterhoff 1996	Upper Pennsylvanian (Stephanian)	0.5 Myr	~10 ⁴ –10 ⁵ yr	Nebraska, Kansas, Oklahoma	Crinoids	Several biofacies recognized in both transgressive and regressive portions of a single stratigraphic cycle; one biofacies restricted to transgressive part (no analog?); collections within biofacies show great deal of variation

Bennington & Bambach 1996	Middle Pennsylvanian (Westphalian)	<10 Myr	0.5–2.5 Myr	Eastern Kentucky	Brachiopods and mollusks	Biofacies (paleocommunity types) are recurrent in four marine incursions, but samples (local paleocommunities) can be statistically significantly different
Olszewski & Patzkowsky 2001	Pennsylvanian-Permian (Stephanian-Wolfcampian)	~2.5 Myr	~0.5 Myr	Nebraska, Kansas	Brachiopods and bivalves	Biofacies remain distinct in each stratigraphic cycle but show a great deal of variation in the taxonomic membership of component collections
Bonuso et al. 2002	Devonian (Givetian)	15 Myr	~1–3 Myr	Central New York State	Corals, brachiopods, mollusks, trilobites, echinoderms, and other groups	Significant taxonomic variation through section; dominant taxa and ecological groups change through section; stasis not observed
Pandolfi 1996	Pleistocene	95 Kyr	~10 ² –10 ³ yr	35 km (PNG)	Reef corals	Persistence in taxonomic composition and species diversity through nine separate reef-building episodes

Source: Modified from Olszewski & Patzkowsky 2001.

^aAbbreviations: Mya = millions of years ago; Myr = millions of years; Kyr = thousands of years.

temporal resolution (Table 2). High-resolution studies focus on communities at less than 1 million year resolution, whereas long-duration studies focus on changes over more than 1 million years. Although this distinction is somewhat artificial, the critical difference is whether evolutionary turnover is expected within the units being compared. High-resolution studies should show little evolutionary change within a time interval, whereas in long-duration studies, even background rates of turnover can result in observable change. In addition, high-resolution studies are usually based on individual collections, whereas long-duration studies are based on compiled lists.

High-resolution studies are noted in Table 2, grouped in the lower portion of the table. Such studies require a stratigraphic framework that allows correlation at levels finer than the time between turnover events (if these events occur in the study interval). One reason that three of the five cited studies in Table 2 (Bennington & Bambach 1996, Holterhoff 1996, Olszewski & Patzkowsky 2001) come from the Carboniferous-Permian period is the strong stratigraphic cyclicity that characterizes these rocks. Despite some of the distinct differences in these studies, none refute the observation that biofacies are recurrent (even in the face of significant environmental change). However, all five studies found that the composition of local communities within a biofacies can be quite flexible and that stability was only evident at a larger geographic scale. Also worth noting is Holterhoff's (1996) report of a nonanalog crinoid assemblage like the nonanalog Quaternary plant assemblages reported by Overpeck et al. (1992), which suggests that communities outside the Pleistocene could also respond to environmental change by reassembling rather than by extinction of member lineages.

Longer-term, soft-bottom marine studies are grouped together at the top of Table 2. These studies range in age from Cambrian to Jurassic (Table 2). These studies focus on durations of more than 10 Myr and generally consist of faunal lists from stratigraphic intervals of less than 1 Myr duration. The spatial scale of these studies usually includes multiple biofacies of an entire basin or platform. A number of generalizations can be made from examining Table 2. First, most studies do show times of elevated taxonomic turnover relative to background rates, although the rates themselves vary greatly. At least some studies (Tang & Bottjer 1996, Patzkowsky & Holland 1997, Olszewski & Patzkowsky 2001) show that episodes of elevated first appearance do not necessarily coincide with, or immediately follow, episodes of disappearance (as in Westrop 1996 and Brett & Baird 1995). In those studies that distinguished biofacies (Westrop 1996, Brett & Baird 1995, Olszewski & Patzkowsky 2001), the history of turnover appeared to differ between biofacies.

In addition, the frequency and magnitude of regional turnover episodes appear to decrease with time (Olszewski & Patzkowsky 2001). Whether this pattern will hold up to future scrutiny is not clear, but it does have implications for global Phanerozoic diversity patterns, which show decreasing rates of extinction and origination through time. This pattern may reflect decreasing susceptibility of ecological communities or their component taxa to turnover events caused by

environmental perturbations of sufficient magnitude. Whether or not this interpretation is corroborated by future work, it makes the point that the fossil record can provide information on intermediate scales that connect ecological and biogeographic processes to paleontological patterns at Phanerozoic scales (Miller 1998).

Quaternary Coral Reef Dynamics

The ecological dynamics of living reef communities observed over yearly to decadal time scales is characterized by fluctuating species composition with changing environmental conditions (Connell 1978, Sale 1988, Tanner et al. 1994, Bak & Nieuwland 1995, Connell et al. 1997). Thus, community structure varies unpredictably over small temporal scales. Similarly, studies at small spatial scales (small areas on single reefs, less than 1 km) have shown convincingly that both fish (Williams 1980, Sale & Douglas 1984, Sale & Steel 1989, Doherty & Williams 1988, Sale 1988, Sale et al. 1994) and corals (Tanner et al. 1994, Connell et al. 1997) show a high degree of variability in community structure. Thus, living coral reefs appear to show a large degree of disorder in community composition at small spatial and temporal scales.

In contrast, results from several recent studies of Quaternary reefs all point to remarkable persistence in taxonomic composition and diversity during multiple episodes of global climate change over the past 500 Kyr (Jackson 1992; Hubbard et al. 1994; Stemann & Johnson 1992; Pandolfi 1996, 1999; Aronson & Precht 1997; Greenstein et al. 1998). Pandolfi (1996, 1999) assembled and analyzed data on species distribution patterns from reef coral assemblages, aged between 125 Kyr and 30 Kyr, from three sites along 35 km of the Huon Peninsula in Papua New Guinea. Persistence in species composition was found among assemblages that lived during nine successive, glacially induced, high-sea level stands (Figure 1) (Pandolfi 1996, 1999). Data on species distribution patterns from reef coral assemblages, aged between 220 Kyr and 104 Kyr, from three sites along 25 km of Barbados also showed persistence in species composition among assemblages that lived during four successive, glacially induced, high-sea level stands. These patterns were shown by use of species relative-abundance data, and the rare taxa showed similar trends to the common taxa (Pandolfi 2000).

Aronson & Precht (1997) and Aronson et al. (2002, 2004) documented a change in the dominant coral in Belize and Panama that occurred recently. In the Belize lagoon, *Acropora cervicornis*, dominant for the past 3000 years in cores, was replaced by *Agaricia tenuifolia* in the 1980s as the dominant coral species. Similarly, in the Bocas del Toro lagoon in Panamá, *Porites* spp., dominant for over 3000 years, also has now been replaced as the dominant coral by *Agaricia tenuifolia*.

These consistent species-distribution patterns demonstrate that Pleistocene reef communities comprised more predictable associations of reef coral species, over broad spatial and temporal scales, than those observed by ecologists on living

reefs at smaller scales. Such broad-scale persistence in community structure is in good agreement with several studies on living reefs of fish (Ault & Johnson 1998, Robertson 1996) and corals (Geister 1977) examined at a scale of less than 1 km, as well as with a recent study that documented broad-scale predictability in living adult coral abundance for over 2,000 km of the Great Barrier Reef, Australia (Hughes et al. 1999). Patterns of persistence in space and time are, thus, well documented for coral reef communities.

Two underlying causes for persistence in coral reef community structure have been offered. Hubbell (1997) interpreted Pandolfi's reef coral data from Papua New Guinea in terms of the unified neutral theory (Hubbell 2001). He asserted that patterns of persistence in community structure could come about as easily by a "law of large numbers" as they could by niche differentiation and limited membership, as advocated by Pandolfi (1996, 1999). However, his comments were tempered by an impression that Pandolfi had used only the common corals in his analysis, when, in fact, patterns were similar whether the analyses were confined to common species or included rare species. Moreover, data analyzed from Barbados showed that patterns in persistence of common taxa were exactly mimicked in the rare taxa, further evidence that large population size is immaterial to persistence in coral reef communities (Pandolfi 2000). The data from Papua New Guinea and Barbados appear to indicate limitations on membership in reef coral associations in space and time and suggest that these associations are not random assemblies of available species.

DISCUSSION

The case studies are derived primarily from the authors' areas of research and provide only a subset of paleontological research that could be brought to bear on the question of community persistence through time. However, they serve to illustrate the following points.

Improving the Exchange Between Paleoecology and Ecology

Many aspects of communities can be described from fossil data, such as richness, species abundances, and trophic interactions, at temporal resolutions ranging from 10^0 to 10^6 years. Useful generalizations about the ecological and evolutionary processes that underlie these patterns depend on our ability to compare different studies. A good deal of confusion has been caused by workers who examined patterns at different geographic, temporal, or taxonomic scales and came to apparently contradictory conclusions. Our intention in this review is not to set down "correct" procedures or standard sampling protocols (of necessity, these must reflect the stratigraphic and taphonomic context of the study), but to clarify the information that can and should be stated explicitly in any study, theoretical or empirical, of community evolution in the fossil record. To compare the results of

different studies, others need to know the spatial and environmental resolution and extent, temporal resolution and duration, and taxonomic and ecomorphic nature of the data. Many of these recommendations already are in use, which reflects broadening recognition of the issues that surround the relationship between the structure of ecological communities and rates of evolution.

First, the spatial resolution and extent of the study should be stated explicitly. How large was the area investigated? In addition, and perhaps more significant, the degree of habitat variability in the area also must be reported. The community of a large, environmentally uniform region may be more comparable to a smaller patch in a more environmentally variable region. When communities of different ages are compared, are the units of comparison individual collections, are they biofacies or paleocommunities that are based on many collections but represent a single habitat, or are they gradients or landscapes that cross multiple habitats? Have habitats been tracked geographically to assess the constancy of species composition through space and time or have they been observed only as recurrent, and temporally separated, sampling intervals within the study area? An additional issue is how biofacies or larger gradients have been identified and whether those of one study are really comparable to those of another study.

Second, the degree of environmental resolution should be considered. Is more than one habitat represented? Are environmental gradients present, and how have such gradients been sampled? What is the range in environmental variability? Is this study conducted within or between habitats?

Third, the temporal resolution and duration of the study should be noted and the degree of time-averaging in individual samples should be included (e.g., Tables 1 and 2). Even a crude estimate can be helpful in providing perspective on the appropriate scale of inferred ecological processes. Stratigraphic horizons, even in some Paleozoic successions, can be resolved at scales of less than 10^6 years, in some cases even representing *in situ* communities buried catastrophically. Stratigraphic resolution is critical to distinguish between intervals of slow background change or stasis and short episodes of rapid turnover. What is the duration of the study? Some Quaternary studies may represent 10^5 to 10^6 years—an interval that is below the resolution of some (not all) deep-time studies. That the results of studies at different scales may have implications for one another is not in dispute, but they cannot be compared directly as if they were equivalent.

Fourth, biological resolution of the study should be determined. Most paleontological studies use taxa—species, genera, or higher groups—as the basic unit of analysis. However, different levels of taxonomic resolution produce very different expectations for patterns of stability through time. Is the study restricted to a single clade, or does it attempt to include all available groups? Alternatively, functional diversity and ecomorphs also can be examined through time and may produce very different patterns than taxonomic analyses.

Fifth, when patterns are reported, basic descriptive data should be included, in addition to derived measures, because such data allows calculation of alternative metrics or statistics as well as assessment of the amount of data available.

Environmental Tracking

The concept of environmental tracking by floras and faunas has had a mixed reception in the ecological literature. On the basis of the data reviewed here, biotas do appear to track climates, but such tracking is certainly influenced by geographic and physicochemical barriers. Environmental tracking is important for understanding long-term ecological patterns because it removes certain high-level taphonomic megabiases in the study of the factors that may influence the patterns; thus, the range of extrinsic environmental variables that must be considered as causative factors is reduced.

Embedded within this issue is the question of species individuality. The clear recognition of Quaternary “nonanalog” floras (Overpeck et al. 1992) begs the question of scale. Miller (1993) argued that environmental tracking was a characteristic of community types rather than specific communities of marine invertebrates. In effect, a “community type” might be considered to be a “biome” in the sense of terrestrial vegetation. Biomes have been shown in both empirical studies (e.g., Ziegler 1990) and modeling studies (e.g., Kutzbach et al. 1998) to approximate climatic boundaries closely and to expand and contract in concert with climatic changes. Species individuality seems most strongly expressed within these biome-level units (DiMichele et al. 2004).

Limits to biome membership may reflect historical patterns of clade origin and distribution (Valentine 1980). Unexpectedly strong relationships between ecological niche and phylogenetic relatedness of species have been documented for extant plants (Prinzing et al. 2001) and were labeled “phylogenetic niche conservatism.” Similar conservatism appears to underlie long-term patterns of within-environment, within-clade, species replacement in Permo-Carboniferous tropical ecosystems (Knoll 1984, DiMichele & Phillips 1996a), rather than such mechanisms as “ecological locking.” This feature is not just a pattern found in plants. Quaternary fossil insects (Coope 1994), both individual species and communities, show strong conformance to shifting climatic conditions. Small Pleistocene mammals exhibit strong patterns of co-occurrence, with little disassociation in response to climate change (Alroy 1999). Depending on the scale of analysis, some marine invertebrate communities also show strong long-term persistence within limits of oceanographic conditions (Jackson 1994; Pandolfi 1996, 2000; Brett & Baird 1995); however, such patterns have not been widely demonstrated for many kinds of marine communities (Jablonski & Sepkoski 1996).

Strong environmental tracking does not require high levels of species interaction. However, some recent studies suggest that interspecific interactions can have strong stabilizing effects. A study of Holocene pollen from eastern North America, for example (Clark & McLachlan 2003), found that species abundances stabilized rapidly after glacial retreat and have remained stable over broad geographic scales, which counters the long-standing view of Holocene forests as randomly assembled and ever-changing species associations. Milchunas et al. (1988) have proposed that feedback in subhumid grassland ecosystems that have a long history of grazing has led to “switching mechanisms” and divergent selection that allow different

species to become dominant under different stress conditions. This pattern contrasts with that in semiarid grasslands, where dominant species become yet more dominant under stress, and convergent selection reigns. The responses to grazing in grasslands with short evolutionary histories involve little feedback and are characterized by individualistic species' responses to grazing pressure. The existence of "switching mechanisms" among different species could lead to a situation in which different dominance patterns occur in an otherwise stable community. Both of these studies conflict with predictions of Hubbell's (2001) "community drift" model, which emphasizes persistent dominance patterns as simply the result of the "law of large numbers," and not a result of interspecific interactions.

Nonetheless, environmental boundaries and species conformance with them may be the single most important cause of long-term persistence of taxonomic associations in the fossil record. At least species-by-environment conformance is much more easily examined in the fossil record than are interspecific interactions. The key to the matter seems to be spatial scale, related directly to environmental scale. As noted by Zeigler et al. (2003), species distributional patterns may be constrained mainly by atmospheric and oceanic circulation patterns, which have sharp boundaries. Identifying the limits to these boundaries and the nature of their change through time is key to understanding the persistence of assemblages of organisms.

CONCLUSIONS

Above we noted that there are four underlying factors that could contribute to the persistence of species assemblages through long periods of geological time. First was the matter of evolved mutualisms. This factor is without a doubt the most difficult to identify in the fossil record (or in modern communities), but some illuminating research has been conducted on the subject. Studies of reef corals (Pandolfi 1996, 2000) suggest limited membership in certain environments, which points to selectivity, possibly the result of biotic interactions. Similarly, studies of temperate tree patterns (Clark & McLachlan 2003) and grasslands (Milchunas et al. 1988) also suggest mutualisms that may lead to community persistence. Patterns of within-clade ecomorphic replacement in late Paleozoic coal-swamp ecosystems (DiMichele and Phillips 1996a) also hint at the possibility that interspecific interactions may partly control replacement dynamics. Plant-insect associations across sudden and protracted environmental shifts indicate that levels and types of herbivory recoup from regional extinction throughout the fossil record (Wilf et al. 2001, Labandeira & Phillips 2002, Labandeira et al. 2002). Much needs to be done in this area, and most of the work will come from neoecology, with results extrapolated to the fossil record primarily through models.

Second is the issue of environmental control. Nearly all the examples given in this review point strongly to the fact that species are neither randomly nor continuously distributed across the landscape. Boundaries to species distribution clearly exist, and many species have very similar, strongly overlapping ranges and limits. This broad pattern is one that permits the recognition of evolutionary-ecological

units and, at the same time, can limit the utility of local studies for global geological temporal correlation. Thus, this situation may be one in which matters of scale, spatial and temporal, can be most clearly seen as important system constraints.

Third is consideration of the effect of historical contingency, which is manifested in biogeographic patterns. Biogeographic limitations lie a level above those placed on species associations by climatic and other environmental factors. Biogeographic factors control the species pool at a fundamental evolutionary level and underlie many of the studies discussed here, without being made explicit, as indicated by the patterns of geographic restriction.

Fourth, the “law of large numbers” has been offered as a null explanation for persistence (Hubbell 2001). This model generally predicts a rapid decrease in community similarity as spatial distance and periods of time increase. The law of large numbers is invoked only when the predictions of other explanations are not borne out. Studies of coral reefs (Pandolfi 2000) and temperate Holocene forest composition (Clark & McLachlan 2003) have challenged this assertion by showing, respectively, that rare taxa can also show persistence within assemblages and that spatial decay in assemblage similarity is not the rule in some biomes. This “law” still needs to be evaluated when claims of community persistence are made.

In conclusion, the fossil record offers considerable evidence for the persistence of species assemblages at many different spatial and temporal scales. It suggests a hierarchy of ecological organization and that variance is not uniformly distributed throughout that hierarchy. Some levels show greater spatial and temporal persistence of patterns than others. The case studies and discussion presented above point to several possible causes for these patterns and provide a range of possibilities and recommendations that we hope will encourage more uniform approaches and increased exchange between paleoecologists and neoecologists in the future.

ACKNOWLEDGMENTS

We appreciate the participation and input of Alistair McGowan and members of the Paleobiology Journal Club during discussion sessions along the way to finalization of this review. This is the Evolution of Terrestrial Ecosystems (ETE) Program Publication No. 121.

**The *Annual Review of Ecology, Evolution, and Systematics* is online at
<http://ecolsys.annualreviews.org>**

LITERATURE CITED

- Alemseged Z. 2003. An integrated approach to taphonomy and faunal change in Shungura Formation (Ethiopia) and its implication for hominid evolution. *J. Hum. Evol.* 44:461–78
- Algeo TJ, Wilkinson BH. 1987. Periodicity of mesoscale Phanerozoic sedimentary cycles and the role of Milankovitch orbital modulation. *J. Geol.* 96:313–22
- Allen TFH, Hoekstra TW. 1992. *Toward a*

- Unified Ecology*. New York: Columbia Univ. Press
- Alroy J. 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 127:285–311
- Alroy J. 1999. Putting North America's end-Pleistocene megafaunal extinction in context: large scale analyses of spatial patterns, extinction rates, and size distributions. In *Extinctions in Near Time: Causes, Contexts, and Consequences*, ed. RDE MacPhee, pp.105–43. New York: Plenum
- Aronson RB, Macintyre IG, Precht WF, Murdoch TJT, Wapnick CM. 2002. The expanding scale of species turnover events on coral reefs in Belize. *Ecol. Monogr.* 72:233–49
- Aronson RB, Macintyre IG, Wapnick CM, O'Neill MW. 2004. Phase shifts, alternative states, and the unprecedented convergence of two reef systems. *Ecol. Monogr.* In press
- Aronson RB, Precht WF. 1997. Stasis, biological disturbance, and community structure of a Holocene coral reef. *Paleobiology* 23:326–46
- Ault TR, Johnson CR. 1998. Spatially and temporally predictable fish communities on coral reefs. *Ecol. Monogr.* 68:25–50
- Bak RPM, Nieuwland G. 1995. Long-term change in coral communities along depth gradients over leeward reefs in the Netherlands Antilles. *Bull. Mar. Sci.* 56:609–19
- Bambach RK, Bennington JB. 1996. Do communities evolve? A major question in evolutionary paleoecology. In *Evolutionary Paleobiology*, ed. D Jablonski, DH Erwin, JH Lipps, pp. 123–60. Chicago: Univ. Chicago Press
- Barry JC, Johnson NM, Raza SM, Jacobs LL. 1985. Neogene mammalian faunal change in southern Asia: correlations with climatic, tectonic and eustatic events. *Geology* 13:637–40
- Barry JC, Morgan ME, Flynn LJ, Pilbeam D, Behrensmeyer AK, et al. 2002. Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan. *Memoir. 3. Paleobiology* 28:1–72
- Baumiller TK, Gahn FJ. 2002. Fossil record of parasitism on marine invertebrates with special emphasis on the platyceratid-crinoid interaction. In *The Fossil Record of Predation. Paleontological Society Papers*, ed. M Kowalewski, PH Kelley, 8:195–209. Knoxville, TN: Paleontol. Soc.
- Behrensmeyer AK, Chapman RE. 1993. Models and simulations of taphonomic time-averaging in terrestrial vertebrate assemblages. In *Taphonomic Approaches to Time Resolution in Fossil Assemblages. Short Courses in Paleontology No. 6*, ed. S Kidwell, AK Behrensmeyer, pp. 125–49. Knoxville, TN: Paleontol. Soc.
- Behrensmeyer AK, Damuth JD, DiMichele WA, Potts R, Sues H-D, Wing SL, eds. 1992. *Terrestrial Ecosystems Through Time*. Chicago: Univ. Chicago Press
- Behrensmeyer AK, Hook RW. 1992. Paleoenvironmental contexts and taphonomic modes. See Behrensmeyer et al. 1992, pp. 14–136
- Behrensmeyer AK, Kidwell SM, Gastaldo RA. 2000. Taphonomy and paleobiology. In *Deep Time. Supplement to Paleobiology Volume*, ed. DH Erwin, SL Wing, 26:103–47. Knoxville, TN: Paleontol. Soc.
- Belyea LR, Lancaster J. 1999. Assembly rules within a contingent ecology. *Oikos* 86:402–16
- Bennington JB, Bambach RK. 1996. Statistical testing for paleocommunity recurrence: Are similar fossil assemblages ever the same? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 127:107–34
- Bobe R, Behrensmeyer AK, Chapman RE. 2002. Faunal change, environmental variability and late Pliocene hominin evolution. *J. Hum. Evol.* 42:475–97
- Bobe R, Behrensmeyer AK, Eck GG, Leakey LN. 2003. A comparative approach to faunal change in the Hadar and Turkana regions. *Am. J. Phys. Anthropol. Suppl.* 36:69
- Bobe R, Eck GG. 2001. Responses of African bovids to Pliocene climatic change. *Paleobiol. Mem.* 27(Suppl. 2):1–47
- Bonuso N, Newton CR, Brower JC, Ivany LC.

2002. Does coordinated stasis yield taxonomic and ecologic stability? Middle Devonian Hamilton Group of central New York. *Geology* 30:1055–58
- Boucot AJ. 1975. *Evolution and Extinction Rate Controls*. Amsterdam: Elsevier
- Boucot AJ. 1978. Community evolution and rates of cladogenesis. *Evol. Biol.* 11:545–655
- Boucot AJ. 1983. Does evolution take place in an ecological vacuum? II. *J. Paleontol.* 57:1–30
- Boucot AJ, Lawson JD, eds. 1999. *Paleocommunities; A Case Study from the Silurian and Lower Devonian*. Cambridge, UK: Cambridge Univ. Press
- Brett CE, Baird GC. 1995. Coordinated stasis and evolutionary ecology of Silurian to Middle Devonian faunas in the Appalachian Basin. In *New Approaches to Speciation in the Fossil Record*, ed. DH Erwin, RL Anstey, pp. 285–315. New York: Columbia Univ. Press
- Brett CE, Ivany LC, Schopf KM. 1996. Coordinated stasis: an overview. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 127:1–20
- Broutin J, Doubinger J, Farhanel G, Freydet F, Kerp H, et al. 1990. Le renouvellement des flores au passage Carbonifère Permien: approches stratigraphique, biologique, sédimentologique. *C. R. Acad. Sci. Paris* 311: 1563–69
- Brown FH. 1994. Development of Pliocene and Pleistocene chronology of the Turkana Basin, East Africa, and its relation to other sites. In *Integrative Paths to the Past*, ed. RS Corruccini, RL Ciochon, pp. 285–312. Englewood Cliffs, NJ: Prentice-Hall
- Buzas MA, Culver SJ. 1994. Species pool and dynamics of marine paleocommunities. *Science* 264:1439–41
- Chave J. 2004. Neutral theory and community ecology. *Ecol. Lett.* 7:241–53
- Clark JS, McLachlan JS. 2003. Stability of forest biodiversity. *Nature* 423:635–38
- Clements FR. 1916. *Plant Succession: An Analysis of the Development of Vegetation*. Washington, DC: Carnegie Inst.
- Coley PD, Barone JA. 1996. Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Syst.* 27:305–35
- Connell JH. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–10
- Connell JH, Hughes TP, Wallace CC. 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol. Monogr.* 67:461–88
- Coope GR. 1994. The response of insect faunas to glacial-interglacial climatic fluctuations. *Philos. Trans. R. Soc. London Ser. B* 344:19–26
- Cottingham KL, Brown BL, Lennon JT. 2001. Biodiversity may regulate the temporal variability of ecological systems. *Ecol. Lett.* 4: 72–85
- Cridland AA, Morris JE. 1963. *Taeniopteris, Walchia, and Dichophyllum* in the Pennsylvanian System of Kansas. *Univ. Kans. Sci. Bull.* 44:71–82
- Damuth JD. 1992. Taxon-free characterization of animal communities. See Behrensmeier et al. 1992, pp. 183–203
- Davis MB. 1986. Climatic instability, time lags, and community disequilibrium. In *Community Ecology*, ed. J Diamond, TJ Case, pp. 269–84. New York: Harper & Row
- de Heinzelin J. 1983. *The Omo Group*. Ter- vuren: Musée R. l' Afrique Central
- deMenocal PB. 1995. Plio-Pleistocene African climate. *Science* 270:53–59
- deMenocal PB, Bloemendal J. 1995. Plio-Pleistocene climatic variability in subtropical Africa and the paleoenvironment of hominid evolution: a combined data-model approach. In *Paleoclimate and Evolution with Emphasis on Human Origins*, ed. ES Vrba, GH Denton, TC Partridge, LH Burckle, pp. 262–88. New Haven: Yale Univ. Press
- Dettman DL, Kohn MJ, Quade J, Ryerson FJ, Ojha TP, Hamidullah S. 2000. Seasonal stable isotope evidence for a strong Asian monsoon throughout the past 10.7 Ma. *Geology* 29:31–34
- DeWoody YD, Swihart RK, Craig BA, Goheen JR. 2003. Diversity and stability in communities structured by asymmetric resource allocation. *Am. Nat.* 162:514–27

- DiMichele WA. 1994. Ecological patterns in time and space. *Paleobiology* 20:89–92
- DiMichele WA, Aronson RB. 1992. The Pennsylvanian-Permian vegetational transition: a terrestrial analogue to the onshore-offshore hypothesis. *Evolution* 46:807–24
- DiMichele WA, Gastaldo RA, Pfefferkorn HW. 2004. Biodiversity partitioning in the Late Carboniferous and Early Permian and its implications for ecosystem assembly. In *Biodiversity*, ed. N Jablonski. San Francisco: Calif. Acad. Sci. In press
- DiMichele WA, Mamay SH, Chaney DS, Hook RW, Nelson WJ. 2001a. An Early Permian flora with Late Permian and Mesozoic affinities from north-central Texas. *J. Paleontol.* 75:449–60
- DiMichele WA, Pfefferkorn HW, Phillips TL. 1996. Persistence of Late Carboniferous tropical vegetation during glacially driven climatic and sea-level fluctuations. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 125:105–28
- DiMichele WA, Phillips TL. 1996a. Clades, ecological amplitudes, and ecomorphs: phylogenetic effects and the persistence of primitive plant communities in the Pennsylvanian-age tropics. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 127:83–106
- DiMichele WA, Phillips TL. 1996b. Climate change, plant extinctions, and vegetational recovery during the Middle-Late Pennsylvanian transition: the case of tropical peat-forming environments in North America. In *Biotic Recovery from Mass Extinctions. Geol. Soc. London Spec. Publ.*, ed. ML Hart, 102:201–21. London: Geol. Soc.
- DiMichele WA, Phillips TL, Nelson WJ. 2002. Place vs. time and vegetational persistence: a comparison of four tropical paleomires from the Illinois Basin at the height of the Pennsylvanian ice age. *Int. J. Coal Geol.* 50:43–72
- DiMichele WA, Stein WE, Bateman RM. 2001a. Ecological sorting during the Paleozoic radiation of vascular plant classes. In *Evolutionary Paleocology*, ed. WD Allmon, DJ Bottjer, pp. 285–35. New York: Columbia Univ. Press
- Doherty PJ, Williams D McB. 1988. The replenishment of coral reef fish populations. *Oceanogr. Mar. Biol. Annu. Rev.* 32:487–551
- Falcon-Lang HJ. 2003. Response of Late Carboniferous tropical vegetation to transgressive-regressive rhythms at Joggins, Nova Scotia. *J. Geol. Soc. London* 160:643–48
- Feibel CS, Brown FH, McDougall I. 1989. Stratigraphic context of fossil hominids from the Omo Group deposits: northern Turkana Basin, Kenya and Ethiopia. *Am. J. Phys. Anthropol.* 78:595–622
- Foote M. 2000. Origination and extinction components of taxonomic diversity: general patterns. *Paleobiology* 26(Suppl.):74–102
- Frakes LA, Francis JE, Syktus JI. 1992. *Climate Modes of the Phanerozoic*. Cambridge, UK: Cambridge Univ. Press
- Gastaldo RA, DiMichele WA, Pfefferkorn HW. 1996. Out of the icehouse into the greenhouse: a late Paleozoic analogue for modern global vegetational change. *GSA Today* 6:1–7
- Geister J. 1977. The influence of wave exposure on the ecological zonation of Caribbean coral reefs. *Proc. 3rd Int. Coral Reef Symp.* 1:23–29
- Gleason HA. 1926. The individualistic concept of the plant association. *Bull. Torrey Bot. Club* 53:7–26
- Golley FB. 1993. *A History of the Ecosystem Concept in Ecology*. New Haven: Yale Univ. Press
- Gotelli NJ, Graves GR. 1996. *Null Models in Ecology*. Washington, DC: Smithsonian Inst. Press
- Graham RW. 1997. The spatial response of mammals to Quaternary climate changes. In *Past and Future Rapid Environmental Changes: The Spatial and Evolutionary Responses of Terrestrial Biota. NATO ASI Ser. I: Global Environmental Change*, ed. B Huntley, W Cramer, AV Morgan, HC Prentice, AM Solomon, 47:153–62. New York: Springer-Verlag
- Greenstein BJ, Curran HA, Pandolfi JM. 1998. Shifting ecological baselines and the demise of *Acropora cervicornis* in the western North

- Atlantic and Caribbean province: a Pleistocene perspective. *Coral Reefs* 17:249–61
- Gunderson LH, Pritchard L, Holling CS, Folke C, Peterson GD. 2002. A summary and synthesis of resilience in large-scale systems. In *Resilience and the Behavior of Large-scale Systems*, ed. LH Gunderson, L Prichard Jr., pp. 249–66. Washington, DC: Island
- Hoffman A. 1979. Community paleoecology as an epiphenomenal science. *Paleobiology* 5:357–79
- Holland SM. 2003. Confidence limits on fossil ranges that account for facies changes. *Paleobiology* 29:468–79
- Holling CS. 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4: 1–23
- Holterhoff PF. 1996. Crinoid biofacies in Upper Carboniferous cyclothems, midcontinent North America; faunal tracking and the role of regional processes in biofacies recurrence. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 127:47–81
- Hubbard DK, Gladfelter EH, Blythell JC. 1994. Comparison of biological and geological perspectives of coral-reef community structure at Buck Island, U.S. Virgin Islands. In *Proc. Colloq. Global Aspects of Coral Reefs: Health, Hazards, and History, 1993*, ed. RN Ginsburg. Miami, FL: Rosenstiel Sch. Mar. Atmos. Sci., Univ. Miami Press
- Hubbell SP. 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Proc. 8th Int. Coral Reef Symp.* 1:33–42
- Hubbell SP. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ: Princeton Univ. Press
- Hughes TP, Baird AH, Dinsdale EA, Molschanivskyj N, Pratchett MS, et al. 1999. Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397:59–63
- Jablonski D, Sepkoski JJ Jr. 1996. Paleobiology, community ecology, and scales of ecological pattern. *Ecology* 77:1367–78
- Jackson JA, Bates RL, eds. 1997. *Glossary of Geology*. Alexandria, VA: Am. Geol. Inst. 4th ed.
- Jackson JBC. 1992. Pleistocene perspectives on coral reef community structure. *Am. Zool.* 32:719–31
- Jackson JBC. 1994. Community unity? *Science* 264:1412–13
- Janis CM, Damuth J, Theodor JM. 2000. Miocene ungulates and terrestrial primary productivity: Where have all the browsers gone? *Proc. Natl. Acad. Sci. USA* 97:7899–904
- Janis CM, Scott KM, Jacobs LL, eds. 1998. *Evolution of Tertiary Mammals of North America*. Volume 1: *Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals*. Cambridge, UK: Cambridge Univ. Press
- Johnson RG. 1960. Models and methods for analysis of the mode of formation on fossil assemblages. *Geol. Soc. Am. Bull.* 71:1075–86
- Kelley PH, Hansen TA. 2001. The role of ecological interactions in the evolution of naticid gastropods and their molluscan prey. In *Evolutionary Paleoecology*, ed. WD Allmon, DJ Bottjer, pp. 149–70. New York: Columbia Univ. Press
- Kidwell SM. 2002. Time-averaged molluscan death assemblages: palimpsests of richness, snapshots of abundance. *Geology* 30:803–6
- Kidwell SM, Holland SM. 2002. The quality of the fossil record: implications for evolutionary analyses. *Annu. Rev. Ecol. Syst.* 33:561–88
- Knoll AH. 1984. Patterns of extinction in the fossil record of vascular plants. In *Extinctions*, ed. M Nitecki, pp. 21–65. Chicago: Univ. Chicago Press
- Kutzbach J, Gallimore R, Harrison S, Behling P, Selin R, Laarif F. 1998. Climate and biome simulations for the past 21,000 years. *Q. Sci. Rev.* 17:473–506
- Labandeira CC. 1998. Early history of arthropod and vascular plant associations. *Annu. Rev. Earth Planet. Sci.* 26:329–77
- Labandeira CC. 2002. The history of associations between plants and animals. In *Plant-Animal Interactions*, ed. C Herrera, O

- Pellmyr, pp. 26–74, 248–61. Oxford: Blackwell Sci.
- Labandeira CC, Johnson KR, Wilf P. 2002. Impact of the terminal Cretaceous event on plant-insect associations. *Proc. Natl. Acad. Sci. USA* 99:2061–66
- Labandeira CC, Phillips TL. 2002. Stem borings and petiole galls from Pennsylvanian tree ferns of Illinois, USA: implications for the origin of the borer and galler functional-feeding groups and holometabolous insects. *Palaeontographica A* 264:1–84
- Lockwood JL, Powell RD, Nott MP, Pimm SL. 1997. Assembling ecological communities in time and space. *Oikos* 80:549–53
- Ludvigsen R, Westrop SR. 1983. Trilobite biofacies of the Cambrian-Ordovician boundary interval in northern North America. *Alcheringa* 7:301–19
- Lyons PC, Darrah WC. 1989. Earliest conifers in North America: Upland and/or paleoclimate indicators? *Palaios* 4:480–86
- Mamay SH, Mapes G. 1992. Early Virgilian plant megafossils from the Kinney Brick Company quarry, Manzanita Mountains, New Mexico. *N. M. Bur. Mines Min. Res. Bull.* 138:61–85
- Marshall CD. 1997. Confidence intervals on stratigraphic ranges with nonrandom distributions of fossil horizons. *Paleobiology* 23: 165–73
- Martini IP, ed. 1997. *Late Glacial and Postglacial Environmental Changes: Quaternary, Carboniferous, Permian, and Proterozoic*. New York: Oxford Univ. Press
- Maurer BA. 1999. *Untangling Ecological Complexity*. Chicago: Univ. Chicago Press
- May RM. 1974. *Stability and Complexity in Model Ecosystems*. Princeton, NJ: Princeton Univ. Press
- McIntosh RP. 1995. H.A. Gleason's 'individualistic concept' and theory of animal communities: a continuing controversy. *Biol. Rev.* 70:317–57
- McKee JK. 2001. Faunal turnover rates and mammalian biodiversity of the late Pliocene and Pleistocene of eastern Africa. *Paleobiology* 27:500–11
- Meyen SV. 1982. The Carboniferous and Permian floras of Angaraland (a synthesis). *Biol. Mem.* 7:1–110
- Milchunas DG, Lauenroth WK, Sala OE. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *Am. Nat.* 132:87–106
- Miller AI. 1998. Biotic transitions in global marine diversity. *Science* 281:1157–60
- Miller W III. 1993. Models of recurrent fossil assemblages. *Lethaia* 26:182–83
- Miller W III. 1996. Ecology of coordinated stasis. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 127:177–90
- Morris PJ, Ivany LC, Schopf KM, Brett CE. 1995. The challenge of paleoecological stasis: reassessing sources of evolutionary stability. *Proc. Natl. Acad. Sci. USA* 92:11269–73
- Olson EC. 1952. The evolution of a Permian vertebrate chronofauna. *Evolution* 6:181–96
- Olson EC. 1958. Faunal of the Vale and Choza: 14. Summary, review, and integration of the geology and the faunas. *Fieldiana Geol.* 10:397–448
- Olson EC. 1980. Taphonomy: its history and role in community evolution. In *Fossils in the Making*, ed. AK Behrensmeier, AP Hill, pp. 5–19. Chicago: Univ. Chicago Press
- Olson EC. 1985. Vertebrate paleoecology: a current perspective. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 50:83–106
- Olszewski TD, Erwin DH. 2004. Dynamic response of Permian brachiopod communities to long-term environmental change. *Nature* 428:738–41
- Olszewski TD, Patzkowsky ME. 2001. Evaluating taxonomic turnover; Pennsylvanian-Permian brachiopods and bivalves of the North American Midcontinent. *Paleobiology* 27:646–68
- Overpeck JT, Webb RS, Webb T III. 1992. Mapping eastern North American vegetation change of the last 18 Ka: No-analogs and the future. *Geology* 20:1071–74
- Overpeck JT, Webb T III, Prentice IC. 1985. Quantitative interpretation of fossil pollen

- spectra: dissimilarity coefficients and the method of modern analogs. *Q. Res.* 23:87–108
- Pandolfi JM. 1996. Limited membership in Pleistocene reef coral assemblages from the Huon Peninsula, Papua New Guinea: constancy during global change. *Paleobiology* 22:152–76
- Pandolfi JM. 1999. Response of Pleistocene coral reefs to environmental change over long temporal scales. *Am. Zool.* 39:113–30
- Pandolfi JM. 2000. *Persistence in Caribbean coral communities over broad spatial and temporal scales*. Presented at 9th Int. Coral Reef Congr., Bali, October 23–27, 2000
- Pandolfi JM, Jackson JBC. 1997. The maintenance of diversity on coral reefs: examples from the fossil record. *Proc. 8th Int. Coral Reef Symp.* 1:397–404
- Patzkowsky ME, Holland SM. 1997. Patterns of turnover in Middle and Upper Ordovician brachiopods of the eastern United States: a test of coordinated stasis. *Paleobiology* 23:420–43
- Patzkowsky ME, Holland SM. 1999. Biofacies replacement in a sequence stratigraphic framework: Middle and Upper Ordovician of the Nashville Dome, Tennessee, USA. *Palaios* 14:310–23
- Peppers RA. 1996. Palynological correlation of major Pennsylvanian (Middle and Upper Carboniferous) chronostratigraphic boundaries in the Illinois and other coal basins. *Geol. Soc. Am. Mem.* 188:1–111
- Peters RH. 1993. *A Critique for Ecology*. Cambridge, UK: Cambridge Univ. Press
- Pfefferkorn HW, Thomson MC. 1982. Changes in dominance patterns in Upper Carboniferous plant-fossil assemblages. *Geology* 10:641–44
- Pfefferkorn HW, Gastaldo RA, DiMichele WA. 2000. Ecological stability during the late Paleozoic cold interval. In *Phanerozoic Terrestrial Ecosystems. Paleontological Society Papers*, ed. RA Gastaldo, WA DiMichele, 6:63–78. Knoxville, TN: Paleontol. Soc.
- Phillips TL, Peppers RA. 1984. Changing patterns of Pennsylvanian coal swamp vegetation and implications of climate control on coal occurrence. *Int. J. Coal Geol.* 3:205–55
- Phillips TL, Peppers RA, DiMichele WA. 1985. Stratigraphic and interregional changes in Pennsylvanian coal-swamp vegetation: environmental inferences. *Int. J. Coal Geol.* 5:43–109
- Pimm SL. 1984. The complexity and stability of ecosystems. *Nature* 307:321–26
- Pimm SL. 1991. *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities*. Chicago: Univ. Chicago Press
- Prinzing A, Durka W, Klotz S, Brandl R. 2001. The niche of higher plants: evidence for phylogenetic conservatism. *Proc. R. Soc. London Ser. B* 268:2383–89
- Robertson DR. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. *Ecology* 77:885–99
- Rothwell GW, Mapes G. 1988. Vegetation of a Paleozoic conifer community. In *Regional Geology and Paleontology of Upper Paleozoic Hamilton Quarry Area in Southeastern Kansas. Guidebook 6*, ed. G Mapes, RH Mapes, pp. 213–23. Lawrence: Kansas Geol. Survey
- Sale PF. 1988. What coral reefs can teach us about ecology. *Proc. 6th Int. Coral Reef Symp.* 1:19–31
- Sale PF, Douglas WA. 1984. Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. *Ecology* 65:409–22
- Sale PF, Guy JA, Steel WJ. 1994. Ecological structure of assemblages of coral reef fishes on isolated patch reefs. *Oecologia* 98:83–99
- Sale PF, Steel WJ. 1989. Temporal variability in patterns of association among fish species on coral patch reefs. *Marine Ecol. Prog. Ser.* 51:35–47
- Scott AC. 1978. Sedimentological and ecological control of Westphalian B plant assemblages from West Yorkshire. *Proc. Yorkshire Geol. Soc.* 41:461–508

- Sheehan PM. 1996. A new look at ecological evolutionary units (EEUs). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 127:21–31
- Simberloff D, Dayan T. 1991. The guild concept and the structure of ecological communities. *Annu. Rev. Ecol. Syst.* 22:115–43
- Smith TM, Shugart HH, Woodward FI, eds. 1997. *Plant Functional Types—Their Relevance to Ecosystem Properties and Global Change*. Cambridge, UK: Cambridge Univ. Press
- Stemann TA, Johnson KG. 1992. Coral assemblages, biofacies, and ecological zones in the mid-Holocene reef deposits of the Enriquillo Valley, Dominican Republic. *Lethaia* 25:231–41
- Tang CM, Bottjer DJ. 1996. Long-term faunal stasis without evolutionary coordination: Jurassic benthic marine paleocommunities, Western Interior, United States. *Geology* 24:815–18
- Tanner JE, Hughes TP, Connell JH. 1994. Species coexistence, keystone species, and succession: a sensitivity analysis. *Ecology* 75:2204–19
- Tilman D. 1999. The ecological consequences of biodiversity: a search for general principles. *Ecology* 80:1455–74
- Tokeshi M. 1993. Species abundance patterns and community structure. *Adv. Ecol. Res.* 24: 111–86
- Ulanowicz RE. 1997. *Ecology, The Ascendent Perspective*. New York: Columbia Univ. Press
- Valentine JW. 1980. Determinants of diversity in higher taxonomic categories. *Paleobiology* 6:444–50
- Van Valkenburgh B. 1995. Tracking ecology over geological time: evolution within guilds of vertebrates. *Trends Ecol. Evol.* 10:71–76
- Vrba ES. 1993. Turnover-pulses, the Red Queen, and related topics. *Am. J. Sci.* 293: 418–52
- Vrba ES. 1995. The fossil record of African antelopes (Mammalia: Bovidae) in relation to human evolution and paleoclimate. In *Paleoclimate and Evolution with Emphasis on Human Origins*, ed. ES Vrba, GH Denton, TC Partridge, LH Burckle, pp. 385–424. New Haven: Yale Univ. Press
- Walker BH. 1997. Functional types in non-equilibrium systems. In *Plant Functional Types*, ed. TM Smith, HH Shugart, FI Woodward, pp. 91–103. Cambridge: Cambridge Univ. Press
- Watkins R, Berry WBN, Boucot AJ. 1973. Why ‘communities’? *Geology* 1:5–8
- Webb T III. 1987. The appearance and disappearance of major vegetational assemblages: long-term vegetational dynamics in eastern North America. *Vegetation* 69:177–87
- Weiher E, Keddy P. 2001. Assembly rules as general constraints on community composition. In *Ecological Assembly Rules. Perspectives, Advances, Retreats*, ed. E Weiher, P Keddy, pp. 251–71. Cambridge, UK: Cambridge Univ. Press
- Westrop SR. 1996. Temporal persistence and stability of Cambrian biofacies: Sunwaptan (Upper Cambrian) trilobites of North America. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 127:33–46
- Westrop SR, Cuggy MB. 1999. Comparative paleoecology of Cambrian trilobite extinctions. *J. Paleontol.* 73:337–54
- Wilf P, Labandeira CC, Johnson KR, Coley PD, Cutter AD. 2001. Insect herbivory, plant defense, and early Cenozoic climate change. *Proc. Natl. Acad. Sci. USA* 98:6221–26
- Willard DA, Phillips TL, Lesnikowska AD, DiMichele WA. 2004. The Calhoun Coal and the persistent organization of Late Pennsylvanian coal-swamp vegetation. *Int. J. Coal Geol.* In press
- Williams D. McB. 1980. Dynamics of the pomacentrid community on small patch reefs in One Tree Lagoon (Great Barrier Reef). *Bull. Mar. Sci.* 30:159–70
- Wing SL, DiMichele WA. 1992. Ecological characterization of fossil plants. See Behrensmeyer et al. 1992, pp. 139–80
- Wing SL, DiMichele WA. 1995. Conflict between local and global changes in plant diversity through geological time. *Palaos* 10: 551–64

- Wing SL, Harrington GJ. 2001. Floral response to rapid warming at the Paleocene/Eocene boundary and implications for concurrent faunal change. *Paleobiology* 27:539–62
- Woodburne MO. 1987. *Cenozoic Mammals of North America*. Berkeley: Univ. Calif. Press
- Zachos J, Pagani M, Sloan L, Thomas E, Billups K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292:686–93
- Ziegler AM. 1990. Phytogeographic patterns and continental configurations during the Permian Period. *Geol. Soc. Mem.* 12:363–79
- Ziegler AM, Eshel G, Rees PM, Rothfus TA, Rowley DB, Sunderlin D. 2003. Tracing the tropics across land and sea: Permian to present. *Lethaia* 36:227–54