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PALEOBIOLOGY, COMMUNITY ECOLOGY, AND SCALES OF ECOLOGICAL PATTERN¹

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Abstract. The fossil record provides a wealth of data on the role of regional processes and historical events in shaping biological communities over a variety of time scales. The Quaternary record with its evidence of repeated climatic change shows that both terrestrial and marine species shifted independently rather than as cohesive assemblages over scales of thousands of years. Larger scale patterns also show a strong individualistic component to taxon dynamics; assemblage stability, when it occurs, is difficult to separate from shared responses to low rates of environmental change. Nevertheless, the fossil record does suggest that some biotic interactions influence large-scale ecological and evolutionary patterns, albeit in more diffuse and protracted fashions than those generally studied by community ecologists. These include: (1) the resistance by incumbents to the establishment of new or invading taxa, with episodes of explosive diversification often appearing contingent on the removal of incumbents at extinction events; (2) steady states of within-habitat and global diversity at longer time scales (10^7 – 10^8 yr), despite enormous turnover of taxa; and (3) morphological and biogeographic responses to increased intensities of predation and substratum disturbance over similarly long time scales. The behavior of species and communities over the array of temporal and spatial scales in the fossil record takes on additional significance for framing conservation strategies, and for understanding recovery of species, lineages, and communities from environmental changes.

Key words: *coevolution; conservation; diversity; escalation; incumbency; interactions; marine communities; paleobiology; paleoecology; Phanerozoic; Pleistocene; terrestrial communities.*

INTRODUCTION

Ecologists and paleoecologists have become increasingly interested in questions of spatial and temporal scale. Regional processes and historical events are now widely recognized as playing vital roles in shaping biological communities (e.g., Ricklefs and Schluter 1993, Brown 1995). The fossil record is by far the richest source of information on the historical events behind extant communities, and, more generally, on the behavior of communities over macroecological and macroevolutionary time scales (10^3 yr or more). Two themes emerge strongly from paleoecological analyses: (1) the individualistic behavior of species and higher taxa, and (2) the biotic interactions that nevertheless can affect large-scale patterns. The apparent contradiction arises from the plethora of spatial and temporal scales that concern paleoecologists.

THE PRESERVATION FILTER

Most paleobiologists operationally define a community as a spatially and temporally recurrent association of species, without implying that those species

behaved as a functional unit or that biotic interactions determined the structure of that association (Dodd and Stanton 1990, Springer and Miller 1990). The localized species assemblages of the fossil record are, however, several steps removed from their once-living sources (see Kidwell and Flessa's 1995 review of factors that govern the fidelity and resolution of the fossil record, from which this brief sketch is drawn).

Fossil communities most often consist of species, or body parts of species, with high potential for fossilization due to a mineralized skeleton or resistant cuticle. Thus, not all members of a community are equally preserved, and accordingly we have literally billions of Ordovician brachiopods and Miocene oak pollen grains, but only a few jellyfish and earthworms. For the readily preserved components of both marine and terrestrial communities, significant transport out of the original life habitat generally affects few individuals, and only a few taxa and habitats are subject to strong transport effects. Further, virtually all species with preservable hardparts tend to be present in local fossil assemblages, commonly in correct rank abundances, although the smaller body sizes are underrepresented. This fidelity is most clearly documented for marine mollusks and leaf assemblages; other benthos and ter-

¹ For reprints of this Special Feature, see footnote 1, page 1319.

restrial vertebrates show consistent patterns but are less studied.

A more insidious limit to the resolving power of the fossil record is the scale of time-averaging, in which fossils from successive time intervals are mixed by physical and biological agents (the latter ranging from trampling by wildebeest to relocation within a marine sediment by burrowing organisms). This process can mix remains from successive generations, obliterating the record of short-term variation and sometimes blending once-discrete communities into composite assemblages. On the other hand, when analyzed carefully time-averaged assemblages can provide an excellent record of the natural range of community composition on the 10^2 – 10^3 yr time scale. Some kinds of communities, such as hard-substratum marine communities and terrestrial macrofloras, hold out promise at finer scales. Furthermore, less time-averaged snapshots can be captured in many settings because sedimentation is episodic and thus can capture short-term events. Time-averaging nonetheless imposes the primary trade-off in the fossil record: a uniquely long temporal perspective but a relatively coarse temporal resolution within it. The resolution is still narrow, however, relative to the average durations of species (10^6 – 10^7 yr). The fossil record thus permits exploration of potential effects of independence and interaction among co-occurring species and higher taxa over long spans of time and large spatial scales.

INDIVIDUALISTIC BEHAVIOR OF FOSSIL SPECIES

Quaternary communities and climatic change

The fossil record of the past 2×10^6 yr, and especially of the past 50 000 yr where dating of local time series is most refined, provides a vivid portrait of continual breakup and reassembly of communities. Best known are the trees of North America: climatic changes over the last glacial–interglacial cycle brought sweeping changes in community composition and dominance patterns. Species did not move as cohesive assemblages but individualistically, and pollen records provide clear evidence for communities with no modern analogs, as well as for the recent assembly of the associations found today (reviews by Birks 1993, T. Webb 1993). For example, the modern boreal forest dominated by spruce and birch formed only ≈ 6000 yr ago, and from 18 000 to 12 000 yr ago spruce grew in association with sedges in a parkland setting; Overpeck et al. (1992) estimate that $>40\%$ of eastern North America was occupied by vegetational associations lacking modern analogs from 16 000 to 11 000 yr ago. Similar patterns have been recorded for the floras of

Europe, South and Central America, Africa, and Australia (recent studies include Bush et al. 1992, Servant et al. 1993, Colinvaux 1996).

Equally striking are the dynamics of insect distributions: exquisitely preserved fossil beetles from glacial lake sediments demonstrate not only that insect associations are as ephemeral as the botanical ones, but that insect–plant associations also recombine. For example, beetle species today found in woodlands occur 12 000 yr ago in open steppe-tundra vegetation that has no modern analog (Coope 1994, Elias 1994). Terrestrial mammals and to a lesser degree herpetofaunas exhibit similar patterns (e.g., Graham 1986, Holman 1993, Potts and Deino 1995).

The fluid nature of communities and the extensive occurrence of communities with no modern analogs have been attributed to two factors, which need not be mutually exclusive: (1) climatic conditions unlike those of the present day (e.g., different combinations of precipitation, evapotranspiration, and temperatures), and (2) differential migration rates among community members in the face of rapid climatic change. Depending on the time scale involved, evidence exists for both arguments, often termed the dynamic equilibrium and disequilibrium hypotheses, respectively. Migration lags are likely on the century time scale, but at the 10^3 -yr time scale seem to be less important. Thus, quantitative changes in floral composition through a series of 3000-yr time slices can be accurately modeled in terms of species-specific tracking of climatic changes without reference to migration lags; furthermore, major occurrences of floras that lack modern analogs do not coincide well with times of maximum rates of vegetation change (e.g., Overpeck et al. 1992; but see Coope 1987 on insects).

Marine communities have not received as much attention but show comparable if less dramatic patterns through the late Cenozoic. Molluscan species shift their geographic ranges along the California coast during Pleistocene glacial–interglacial cycles to produce assemblages that have no modern counterparts (Valentine and Jablonski 1993). Associations differ for each cycle, ruling out a simple alternation between stable states (see Malatesta and Zarlenga [1986] on the Mediterranean, where glacial faunas are more fully documented than in the interglacial-dominated Eastern Pacific record; and Buzas and Culver [1994] on foraminiferal assemblages of the Western Atlantic coast). Indo-Pacific reef species also appear to shift independently over glacial–interglacial cycles, with much local extinction but very few species lost from the regional pool (see Valentine and Jablonski 1993). Dominant framework-builders may retain prevalence and zonation patterns within a region over several 10^3 -yr climatic cycles (Jackson 1992, Budd et al. 1996), which, as discussed

below, may indicate the exclusion by incumbents of alternative occupants (Jackson 1994a). For those localities where a broader faunal spectrum has been detailed (e.g., Kenya, Aldabra, Hawaii), such stability in coral dominants is not accompanied by constancy of their molluscan associates (Paulay 1991).

Large-scale patterns

Individualistic behavior of species and higher taxa can also be detected in the fossil record over larger scales of 10^6 – 10^7 yr, but the situation is more complicated because this time frame encompasses a broad spectrum of both environmental and biotic changes. For mid-Paleozoic marine invertebrates of 350×10^6 yr ago, benthic communities and regional faunas persist for 5 – 10×10^6 yr with rather limited species loss and introduction (65–80% species persistence), with new species tending to be closely related to coexistent or earlier community members; abrupt and extensive turnovers occur in concert with major environmental changes (Brett and Baird 1995). DiMichele (1994) discusses similar patterns in tropical Carboniferous floras. Boucot (1990) has argued that a pattern of community stasis and reorganization is the rule over even longer time spans, for which he names “ecologic-evolutionary units.”

These temporal patterns have been interpreted as standing in stark contrast to those described above for the late Cenozoic, with Paleozoic marine and terrestrial communities permitted by milder environmental fluctuations to become more tightly integrated. This hypothesized integration has been invoked, in turn, as the basic mechanism behind the evolutionary stasis seen in so many fossil species (e.g., Hoffman 1978, DiMichele 1994, Morris et al. 1995). Such an “ecological-locking” interpretation, with communities at equilibrium for some millions of years and disrupted by environmental changes that clear the way for a brief episode of rapid evolutionary change, has been proposed several times: e.g., Beerbower (1953), in strikingly similar fashion though couched in the chronofauna concept, and Vrba (1985), in terms of her turnover-pulse hypothesis (see W. Miller 1993a for comparisons).

These claims for tighter community integration during the Paleozoic must be treated with caution, however. The broad patterns of species persistence and replacement are equally consistent with individualistic behaviors under situations of lesser environmental change, and so the alternative hypotheses need to be tested rigorously. Gradient analyses of Paleozoic marine assemblages, for example, are similar to those for post-Paleozoic and Recent seas, with broadly overlapping species distributions; abundance curves are generally coincident only at sharp environmental transi-

tions and thus provide little evidence for discrete, tightly bound ecological units (e.g., Springer and Miller 1990, Lafferty et al. 1994, Patzkowsky 1995). W. Miller (1993b) argues that the fossil assemblages seen to track shifting environments are really broader “community types” not strictly comparable to individual communities of living organisms.

Regarding mechanisms for temporal stability, Jackson (1994b) suggests that the major climatic changes that drive biotic turnovers might also impose a filter favoring eurythermal species; these would then persist, because their limits are not exceeded, over subsequent climatic oscillations (see also Stanley 1986). The contention that replacements occur mainly along phylogenetic lines also needs rigorous analysis; Aberhan (1993), who finds most replacements in the early Mesozoic to involve unrelated ecological equivalents, suggests that such lineage-bound patterns, when they occur, reflect biogeographic rather than community-based constraints.

Evolutionary faunas and floras at the global scale

At very large time scales of 10^8 yr, communities appear to combine into yet larger units: evolutionary faunas and floras (Sepkoski 1991a, 1992). The three “great” evolutionary faunas of the Phanerozoic oceans are weakly bounded sets of taxa that share similar (but not identical) histories of diversification and decline over tens to hundreds of millions of years. These are designated the Cambrian, Paleozoic, and Modern (Mesozoic-Cenozoic) Faunas, according to their times of maximum diversity (Fig. 1). On land, Niklas et al. (1983) recognized four evolutionary floras among vascular plants, and Benton (1985) identified three evolutionary faunas among tetrapod vertebrates.

Each marine evolutionary fauna appears to have its own characteristic level of diversity, increasing in stepwise succession (Fig. 1), and characteristic rates of origination and extinction, decreasing in turn (Sepkoski 1991a). Each also appears to have a distinct ecological style: the Cambrian Fauna with generalized detritus- and suspension-feeders and low levels of alpha and beta diversity; the Paleozoic Fauna with complexly tiered epifaunal suspension-feeders and intermediate alpha and beta diversities; and the Modern Fauna with abundant shell-crushing predators and infaunal suspension- and deposit-feeders and highest diversities (Vermeij 1987, Sepkoski 1991a, Bambach 1993) (Fig. 2).

At the community level, the evolutionary faunas dominate different marine habitats as they succeed one another through time. Members of the Cambrian fauna are ubiquitous across the shelf during the Cambrian Period but become progressively more restricted to outer shelf and basinal habitats during the Ordovician,

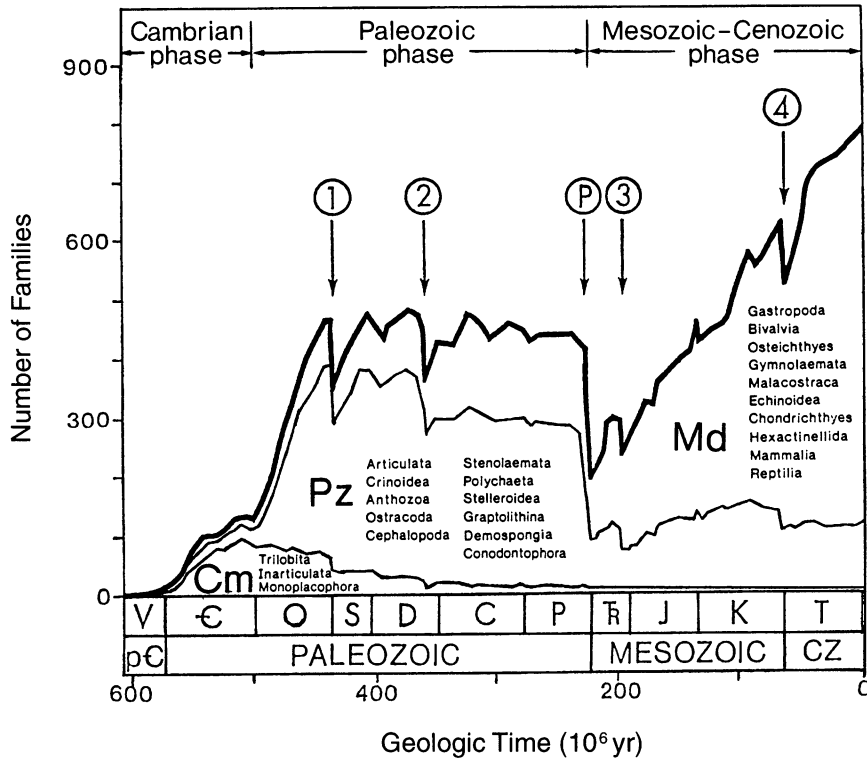


FIG. 1. Diversity of marine animal families through the Phanerozoic, and the three Evolutionary Faunas. Arrows above the curve identify the five major mass extinctions of the Phanerozoic: P = end-Permian; 1 = end-Ordovician; 2 = late Devonian (Frasnian); 3 = end-Triassic; 4 = end-Cretaceous. Fields below the heavy curve delimit diversity histories of the three Faunas: Cm = Cambrian fauna; Pz = Paleozoic fauna; Md = Modern fauna; the principal classes in each fauna are listed. V = Vendian, followed by the periods Cambrian, Ordovician, Silurian, Devonian, Carboniferous, Permian, Triassic, Jurassic, Cretaceous, Tertiary (followed by Quaternary, not labelled); CZ = Cenozoic. From Sepkoski (1992), copyright 1992 by Columbia University Press. Reprinted with permission of the publisher.

when the Paleozoic fauna diversifies and becomes dominant in shelf environments (see Sepkoski 1991b, 1992). Also during the Ordovician, the early members of the Modern fauna rise to dominance in very shallow habitats, then slowly expand into the shelf zone through the remainder of the Paleozoic (and also into deeper, off-shelf environments by the mid-Paleozoic). The end-Permian mass extinction eradicated communities dominated by elements of the Paleozoic fauna, and the Mesozoic-Cenozoic fossil record shows mollusk-dominated communities in the great majority of shelf environments. However, even as late as the Cretaceous, outer-shelf habitats retained prominent epifaunal suspension-feeders reminiscent of the ecological modes, although not the taxa, of Paleozoic seas (Jablonski et al. 1983).

The preceding summary emphasizes the cohesiveness of marine evolutionary faunas, but there is ample mixing at this largest scale of analysis as well. By the Late Ordovician, for example, some bivalve-dominated communities occur in offshore environments (A.I. Mil-

ler 1988, 1989) and some nearshore communities still contain diverse trilobites (Westrop et al. 1995); moreover, lingulid brachiopods, remnants of the Cambrian fauna, dwell even today in tropical intertidal settings. Furthermore, the introduction of elements of the Modern Fauna in Paleozoic communities appears to be a species-by-species process rather than whole-fauna replacements when examined in detail (e.g., Bretsky and Klofak 1986). Thus, the degree of “ecological locking” within evolutionary faunas is limited. As discussed below, the interactions that might underlie the environmental patterns need not be at the level of whole evolutionary faunas or communities. Instead, the pattern and rate of change in community dominance across the shelf can be generated with numerical models that incorporate clade-specific rates of species-level evolutionary turnover and assume incumbent advantage (Sepkoski 1991b; also Valentine 1990a, b, Valentine et al. 1991). These models turn out to be virtually identical to Lotka-Volterra equations that adequately describe the changes in global dominance and diversity

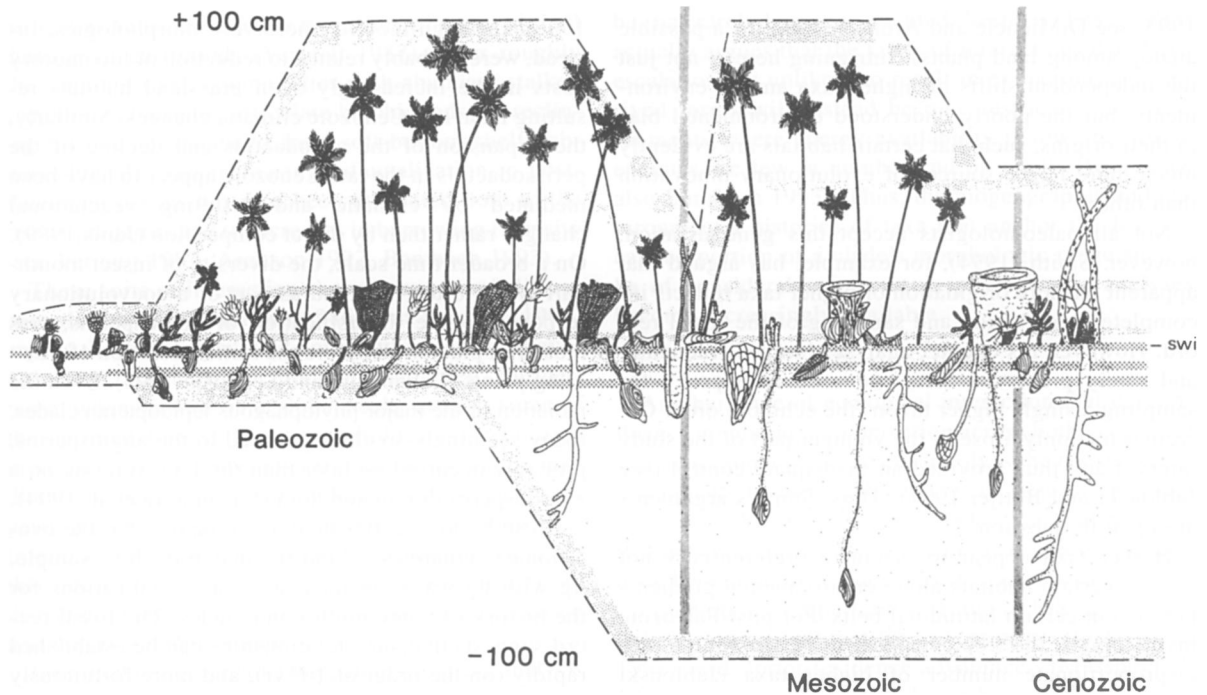


FIG. 2. History of the tiering, or vertical ecological structure, of shallow-water benthic marine communities. Early Paleozoic communities, dominated by the Cambrian Fauna showed little breadth or complexity in tiering patterns (see Fig. 1); occupation of space above and below the sediment-water interface (swi) increased through the Paleozoic, with stalked echinoderms, corals, bryozoans, and other groups extending above the sediment and mollusks and arthropods burrowing into it. The Mesozoic was a time of maximum tiering breadth, followed by a decline of epifaunal forms in the Cenozoic. Dashed lines represent estimated maximum burrowing and elevation depths through time; vertical lines are boundaries between geologic eras. After Ausich and Bottjer (1991). Reprinted with the permission of the *Journal of Geological Education*.

among evolutionary faunas with very diffuse negative interactions posited (see Sepkoski 1991a).

Biotic interchanges and habitat shifts

At regional scales, intermediate between the local community and the global biota, paleobiological invasions offer further insight into the behavior of communities over extended time spans. Because these invasions were commonly mediated by sea-level fluctuations or tectonic events that trigger climatic and other long-term environmental changes, many are difficult to evaluate in terms of community integration: changes in the receiving biota might be driven by any combination of biotic and physical factors. Most invasions recorded in the fossil record, however, enrich biotas instead of triggering extinctions (Vermeij 1991a). No invasion-related extinctions have been documented in studies of the marine trans-equatorial, trans-Arctic, or trans-Pacific interchanges of the late Cenozoic (Vermeij 1991a, b). Invasions of North American and African mammal species appear to trigger no extinctions in Asian faunas (Barry et al. 1991, Flynn et al. 1991), and neither have invasions of Eurasian mammals into

North America (Van Valkenburgh and Janis 1993). In the Great American Interchange created by the uplift of the Panama land bridge, the initial exchange was symmetrical; extinction percentages were similar in the native faunas of both continents (Marshall et al. 1982) and probably related to global climatic changes with the onset of glacial conditions. The prolific diversification of North American immigrants in South America, which imparts an asymmetric flavor to the Interchange, may also have resulted from climatic changes and the expansion of savanna habitats in the southern continent rather than by any intrinsic competitive advantage of the immigrants (S. D. Webb 1991, Vrba 1993).

Many other clades have a clear geographic and environmental component to their histories, and again independence more than cohesion appears to be the rule when analyzed at time scales under 10^8 yr. For benthic marine organisms, higher taxa (i.e., orders and above) tend to originate in onshore environments and spread individualistically across the shelf over tens of millions of years (see Jablonski and Bottjer 1990, 1991; also A. I. Miller 1990, Crimes and Droser 1992, Droser et al.

1993; see DiMichele and Aronson 1992 for a possible analog among land plants). Intriguing here is not just the independent shifts of higher taxa among environments, but the poorly understood environmental bias in their origins, such that certain habitats are evidently much more fertile sources of evolutionary innovation than others.

Not all paleontologists accept this generalization, however. Smith (1994), for example, has argued that apparent onshore origination of higher taxa reflects incomplete preservation and sampling of the fossil record. However, his counter-analyses lumped frequently and rarely preserved taxa, and used as a proxy for sampling a single higher taxon (the echinoid order *Calycina*) that only arose in the younger part of the study interval and thus provided an inadequate control (see Jablonski and Bottjer 1991). Thus, Smith's arguments are open to question.

Higher taxa appear to originate preferentially not only in certain habitats along environmental gradients but also in certain latitudinal belts. For post-Paleozoic invertebrates, the tropics appear to be the source of a disproportionate number of higher taxa (Jablonski 1993). At lower taxonomic levels, a strong latitudinal origination pattern is not obvious among marine invertebrates, but the biogeography is clearly not static (e.g., Crame 1993; and see Vermeij 1991*b* on the late Cenozoic assembly of today's North Atlantic marine fauna).

POSITIVE AND NEGATIVE INTERACTIONS

Despite the individualistic behavior of species and clades across a spectrum of spatial and temporal scales, the fossil record does suggest that biotic interactions influence some large-scale ecological and evolutionary patterns. However, these interactions appear to be more diffuse and protracted than those generally studied or invoked by community ecologists, and many former instances of biotic interaction have been subject to reinterpretation in recent years. Thus, intertaxon patterns from the fossil record have interesting implications for how ecological processes can shape biotas on time scales $>10^6$ yr.

Coevolution

The loose and dynamic organization of communities seen over geologic time scales raises intriguing questions on the nature of coevolution (e.g., reciprocal evolutionary responses between predator and prey). Some long-held scenarios of ecological interaction have not withstood closer scrutiny. For example, fast-running, long-legged ungulates evolved some 20×10^6 yr before the appearance of the pursuit carnivores that were supposed to engage them in a coevolutionary arms race through the Cenozoic (Janis and Wilhelm 1993, Janis

1996); the high-mobility herbivore morphologies, instead, were probably related to reduction of locomotory costs in the increasingly open grassland habitats resulting from late Cenozoic climatic changes. Similarly, the expansion of the artiodactyls and decline of the perissodactyls in the late Cenozoic appear to have been mediated by climatic and resulting vegetational changes rather than by direct competition (Janis 1989). On a broader time scale, the diversity of insect mouthpart types, often regarded as part of a coevolutionary response to the diversification of angiosperms, was mostly in place well before the initial radiation of flowering plants (Labandeira and Sepkoski 1993). Even the radiation of the major phytophagous lepidopteran clades, today seemingly so closely linked to the angiosperms, probably occurred no later than the Late Jurassic on a gymnosperm-dominated flora (Labandeira et al. 1994).

Close biological ties do exist in nature, but the evolutionary dynamics behind the match of, for example, fig with fig-wasp are unclear, as are implications for the history of communities and clades. The fossil record suggests that such relationships can be established rapidly (on the order of 10^3 yr), and more fortuitously than generally assumed. Much apparent precision could arise by interaction with a series of ecologically similar but phylogenetically diverse, and biogeographically labile, partners or enemies (e.g., Futuyma 1986). Thus, phytophagous insects have tended to be conservative in their affiliation with a host taxon, but detailed phylogenies usually show only weak correspondence between insects and hosts (Farrell and Mitter 1994). Similarly, host-specific pairings of marine herbivores and plants have repeatedly arisen in the course of invasion by one member or the other of the association during the Pliocene or later, suggesting opportunism rather than prolonged coevolutionary specialization as an important pathway (Vermeij 1992). Intimate biological associations between extant species are thus not strong evidence for the stability of their communities.

Escalation

The fossil record still suggests that diffuse interactions have profoundly affected at least some portions of biotas over very long time scales. The most striking examples have been grouped by Vermeij (1987, 1994) under the hypothesis of escalation, which holds that biological hazards have become increasingly severe over geologic time, with selection imposed by enemies (predators, competitors, and dangerous prey) driving long-term evolutionary trends in morphology, ecology, and behavior. For example, the diversification of shell-crushing predators among marine benthos during the late Mesozoic and into the Cenozoic was accompanied by an increase in antipredatory morphologies in bivalves, gastropods, and perhaps shelled cephalopods,

as well as an increase in the frequency of repaired shell damage in gastropods (Vermeij 1987). Over roughly the same interval, communities with abundant stalked crinoids, ophiuroids, articulate brachiopods, or reclining bivalves disappeared from soft-bottom shelf habitats (Fig. 2). The increasing infaunalization in post-Paleozoic oceans has also been attributed both to the rise of predators and to increases in burrowing intensity (see Vermeij 1987, Aronson 1992, Bambach 1993).

These sorts of interactions have been termed diffuse coevolution (e.g., Futuyma 1986), but Vermeij (1994) argues that escalation need not entail a reciprocal evolutionary race between predators and prey. Furthermore, when viewed on a global scale, at least some of the antipredatory shifts in morphology arise through increases in among-species variance rather than as unidirectional trends (e.g., D. J. Miller 1993 on muricid gastropods). Roy's (1994) analysis of aporrhaid gastropods does suggest a shift in modal morphology, but this occurs by differential origination within a broad distribution established early in the history of the group and not as a simple trend.

One unexplored area in the paleobiological analysis of large-scale biotic interactions is the extent to which global diversity patterns mirror ecological dominance. In the best studied example, cheilostome bryozoans, which arose in the mid-Mesozoic, today tend to out-compete the more ancient cyclostome bryozoans, but this ecological relationship did not give rise to reciprocal diversity patterns through time. On a global scale, cheilostomes became dominant on a percentage basis without any absolute decline in the number of cyclostome families or species (Lidgard et al. 1993). These and a few other studies suggest that replacements among major groups may sometimes be played out in terms of abundances without exact parallels in taxonomic diversity patterns; more analyses incorporating both kinds of data are sorely needed (Vermeij 1987; see also A.I. Miller 1989, who did find a parallel in Paleozoic bivalves; Westrop et al. [1995] on dilution rather than decline of trilobites in Ordovician communities, and Wing et al. [1993] on an early stage in the rise of the angiosperms).

Precise mechanisms thus remain unclear for the broad, multiclade patterns that unfolded over tens of millions of years to give rise collectively to the Mesozoic Marine Revolution. Despite the variable dynamics noted above, Vermeij (1987, 1994) and Aronson (1992) emphasize the efficacy of phyletic responses and the long-term ecological consequences of short-term interactions. Allmon (1994), taking a more punctuational view, speculates that escalation is shaped by differential speciation rates among variously armored species within a clade (see also Roy 1994). Differential extinction of less escalated taxa is intuitively appealing

but has rarely been documented. Vermeij (1987, 1994) actually argues that the kinds of interactions that drive escalation are unlikely to result in extinction; less derived forms will instead become restricted "to environments where energy availability is low and where enemies are few in number and of small effect" (see also Bambach 1993). Thus, the biogeographic and environmental histories of taxa that anchor the less escalated portion of a clade's morphologic range should be of considerable interest as phylogenetic analyses become increasingly available.

INCUMBENCY

Another style of ecological interaction that may influence community composition across both ecological and evolutionary time scales involves the resistance by incumbents to the establishment of new or invading taxa (e.g., Valentine 1980, 1990a, Van Valen 1985, Rosenzweig and McCord 1991). The precise mechanism behind such incumbency effects, variously termed "pre-emptive competition" (Hallam 1987), "home-field advantage" (Pimm 1991), "priority effect" (Case 1991), and "prior-residence advantage" (Massot et al. 1994), remains uncertain. Incumbency effects could impart long-term structure to communities even if the co-occurrences themselves were maintained mainly by shared environmental tolerances. Once a taxon becomes dominant, mediated perhaps by climatic change, it would tend to exclude new arrivals or re-invasions by equally suitable or even superior potential inhabitants. This has been suggested by Jackson (1992, 1994b) for the coral *Acropora* on Caribbean reefs over the past 500 000 yr. However, the wealth of well-documented Pleistocene range shifts and human-mediated invasions seems at odds with these large-scale paleontological patterns. Thus, Simberloff (1986), who surveyed insects for both successful and failed invasions, concluded that success depends more on habitat requirements of the immigrant than on the composition of the target community (see also Carlton and Geller 1993). This is consistent with Coope's (1995) finding that Pleistocene beetles enter whatever modern community corresponds to their climatic tolerances.

The strongest paleontological evidence for the power of incumbency lies in the aftermath of mass extinctions. The classic example is the early Cenozoic radiation of mammals following the demise of the dinosaurs and other "reptilian" groups after $\approx 150 \times 10^6$ yr of very modest coexistence: mammals, which had evolved 16 Linnean orders (read broadly defined guilds) during their Mesozoic history, generated at least 26 new orders, from bats to whales, during the first 15×10^6 yr following the end-Cretaceous mass extinction (see Stucky and McKenna 1993). An intriguing aberration occurs in South America, where the main Paleocene

predators were a startling assemblage of boid snakes (up to 10 m long), flightless phorusrhacoid birds (up to 3 m tall), and terrestrial crocodylians (Albino 1993); Eocene predators in North America also included large flightless birds (e.g., *Diatryma*) and terrestrial crocodiles. Benton (1991) discusses several additional instances of extinction-mediated diversifications in the terrestrial fossil record, and marine rebounds show similar patterns: in reef communities, for example, the new dominants typically were long-standing minor constituents of the pre-extinction reef biota.

Interactions can have more subtle effects on diversification patterns. A.I. Miller and Sepkoski (1988), employing the same models used to analyze evolutionary faunas, found that marine bivalve genera follow a steady, exponential trajectory through most of the group's history, a pattern generally taken to indicate unimpeded diversification. However, the dramatically higher diversification rates seen during their initial Ordovician radiation and immediately following the end-Permian and end-Cretaceous mass extinctions suggest that the long-term bivalve expansion rate was actually damped by interactions with other marine organisms, since the steady background increase in bivalves themselves did not slow their diversification. The nature of those interactions among species of different clades, and the temporal and spatial scale at which they operate, is still poorly understood.

The role of incumbency in impeding diversification is also seen in the fossil record of invasions. Most biotic interchanges have been asymmetrical, but the imbalance rarely seems attributable in any straightforward way to the competitive ability of the invaders. Instead, large-scale extinctions of species before the onset of interchange renders some biotas especially prone to invasion (Vermeij 1991a). Clearing away some incumbents evidently paves the way for the entry of new taxa. Such asymmetrical interchanges need not be province-wide, but instead can vary among habitats. Thus, with the uplift of the Panama land bridge, rain forest plants, mammals and birds moved largely south to north, but montane plant and mammal species moved largely north to south (Vermeij 1991a; see also S.D. Webb 1991). This reinforces the view that nonreciprocal interchanges arise from the contingencies of history and local ecologies rather than the province-level competitive superiorities once evoked to explain such patterns.

The apparent invasibility of many present-day ecological communities and the fluidity of Pleistocene assemblages contrast strikingly with the dinosaur-mammal pattern and other macroevolutionary situations in which diversification seems contingent on extinction of incumbents. More work is needed on the asymmetry of interchanges to confirm that incumbency plays a role

on the intermediate taxonomic and temporal scale of biotic interchanges, and on the roles of disturbance, incumbency, and standing diversity in excluding invaders on ecological time scales (a clear pattern has not emerged, see Valentine and Jablonski 1993, Robinson et al. 1995 for recent discussions). The present data certainly raise doubts about smooth extrapolation of models or predictions across scales.

Steady-state diversity

The most intriguing evidence that biotic interactions may have a role in the long-term structuring of communities involves steady states in taxonomic diversity at both local and global levels. Global numbers of skeletalized marine families and genera exhibit a 200×10^6 yr plateau during the Paleozoic (e.g., Sepkoski 1991a, 1992, 1994) (Fig. 1). This plateau was punctuated at least twice by major mass extinctions that were followed by rapid rediversifications ("rebounds") that ceased when previous diversity levels had been reached (Sepkoski 1991a, 1992). Indeed, individual clades (e.g., orders) through the Paleozoic rarely exhibit equilibrium diversities; only their ensemble does. (A similar plateau, again with individual clades showing little tendency towards equilibrium, may occur in Cenozoic mammals of North America; Van Valkenburgh and Janis 1993, Alroy 1996.) This, and the approximately logistic trajectory of recovery from repeated extinction events, suggests the operation of a dynamic equilibrium mediated by biotic interaction. Still not understood is why steady-state diversities in the fossil record are achieved and maintained by decreased origination rates alone, rather than the reciprocal behavior of origination and extinction as typically modelled (see Van Valen 1985, Gilinsky and Bambach 1987, Maurer 1989).

The global marine diversity pattern is paralleled by community-level species and genus diversities, although the imperfect match suggests that changes in provinciality may also contribute to global trends (e.g., Valentine 1990b, Signor 1994). Temporal trends in beta diversity for the Paleozoic marine biota paralleled alpha diversity, suggesting increased habitat specificity between the Cambrian and Paleozoic evolutionary faunas but no continuous change within the latter (Sepkoski 1988). This refutes the generality of Whittaker's (1977) expectation of positive feedback in diversification with organisms continually providing resources for yet more organisms to exploit (more recently, Rohde 1991; but see Rosenzweig 1995:301).

CONCLUSION

For a time, paleoecology as a field lost sight of its most powerful aspect: its temporal perspective. The ability to track the origin and fates of species and higher

taxa as well as their associations in an environmental context places paleoecology squarely "at the cusp of evolutionary biology and ecology" (A. I. Miller 1993: 410). Paleocological research has yielded surprises for neontologists and paleontologists alike, such as the ephemeral nature of plant, insect, and molluscan associations through the climatic fluctuations of the Pleistocene. We are only beginning to understand which aspects of ecological structure are stable over geologic time scales, and thus transcend the fluid associations that we ordinarily term communities. A portrait is beginning to emerge of how these major attributes of ecological associations have themselves changed through time and how this has been driven not only by climate but also by the evolution of constituent taxa. We have argued that ecological interactions are important but need not be played out on the temporal and spatial scales generally studied by ecologists. Any community is a dynamic composite of widely and narrowly distributed taxa, so that the strength and persistence of interactions must depend on the respective biodistributional attributes of participant taxa (geography, bathymetry, altitude, etc.) and how they change through time; such questions and many others can be addressed directly using the fossil record.

Evolution certainly does occur within a biotic context, and the ecological attributes of organisms demonstrably affect evolutionary patterns (e.g., Vermeij 1987, Stanley 1990, Jablonski 1991, 1995, Allmon 1994, Van Valen 1994). A new "evolutionary paleoecology" is emerging that entails a host of new approaches to the analysis of large-scale patterns in both time and space. The historical perspective is of more than academic interest as conservation issues become increasingly urgent. As Jackson (1992:727) states, "it is essential to know what we are trying to conserve," and the fossil record provides direct evidence on how communities and taxa respond to changes in climatic and other environmental variables (e.g., Jablonski 1991, 1995, Graham 1992, Coope 1995). Management policies can be informed by our growing understanding of the behavior of species and their associations across a hierarchy of spatial and temporal scales. Uniformitarian doctrine notwithstanding, the past is the key to the present, and to the future as well.

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