

BIOTIC INTERACTIONS AND MACROEVOLUTION: EXTENSIONS AND MISMATCHES ACROSS SCALES AND LEVELS

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Received October 5, 2007

Accepted December 11, 2007

Clade dynamics in the fossil record broadly fit expectations from the operation of competition, predation, and mutualism, but data from both modern and ancient systems suggest mismatches across scales and levels. Indirect effects, as when antagonistic or mutualistic interactions restrict geographic range and thereby elevate extinction risk, are probably widespread and may flow in both directions, as when species- or organismic-level factors increase extinction risk or speciation probabilities. Apparent contradictions across scales and levels have been neglected, including (1) the individualistic geographic shifts of species on centennial and millennial timescales versus evidence for fine-tuned coevolutionary relationships; (2) the extensive and dynamic networks of interactions faced by most species versus the evolution of costly enemy-specific defenses and finely attuned mutualisms; and (3) the macroevolutionary lags often seen between the origin and the diversification of a clade or an evolutionary novelty versus the rapid microevolution of advantageous phenotypes and the invasibility of most communities. Resolution of these and other cross-level tensions presumably hinges on how organismic interactions impinge on genetic population structures, geographic ranges, and the persistence of incipient species, but generalizations are not yet possible. Paleontological and neontological data are both incomplete and so the most powerful response to these problems will require novel integrative approaches. Promising research areas include more realistic approaches to modeling and empirical analysis of large-scale diversity dynamics of ostensibly competing clades; spatial and phylogenetic dissections of clades involved in escalatory dynamics (where prey respond evolutionarily to a broad and shifting array of enemies); analyses of the short- versus long-term consequences of mutualistic symbioses; and fuller use of abundant natural experiments on the evolutionary impacts of ecosystem engineers.

KEY WORDS: Competition, extinction, mutualism, predation, speciation.

Organisms interact with members of other species and clades all the time. Competition, predation, parasitism, and mutualism have been documented in all major environments, and each interaction type is recorded in the geologic past. More subtle, or at least less clearly reciprocal, interactions are also pervasive: corals and trees structure their respective reef and forest environments but are not directly affected by all of the organisms dwelling there. Although these and other interactions have been heavily studied within populations and communities, their macroevolutionary consequences are poorly understood. Clades are said to interact when interactions between their constituent organisms, populations, or species

impinge significantly on speciation, extinction, morphological variety, and/or spatial deployment on one or more of those clades. However, the local and short-term existence of biotic interactions does not demonstrate their overriding role at large spatial and temporal scales, or in molding species- and clade-level dynamics (e.g., Ricklefs 2004, pp. 5–6; Jablonski 2007). In short, we lack a powerful theory for how lower-level processes cascade upwards to clade-level dynamics, and vice versa.

Much of the fossil record—for example, the tendency for species to respond individually to climate changes, the waxing and waning of clades in association with tectonic and

oceanographic events, and the abundant evidence for externally triggered mass extinctions—seems inconsistent with a world shaped over the long term primarily by biotic interactions. Nonetheless, many macroevolutionary patterns in the modern biota and in the geological past are difficult to interpret without invoking positive or negative interactions with species in other clades. Despite the enormous literature on biotic interactions in modern and ancient systems, biotic factors are poorly understood as macroevolutionary agents. This shortcoming derives at least in part from a lack of integration across fields: on one hand, many macroevolutionists have simply ignored the potential role of biotic interaction, or barely moved beyond specific examples and broad consistency arguments, and on the other hand few microevolutionists and ecologists have gone beyond simple extrapolation from their hard-won, but short-term, observations.

I will not solve these problems here, but hope to stimulate the necessary integration across scales and hierarchical levels. A scattered but voluminous body of data, models, and informed speculation suggests that such an integrated approach will be more profitable than the predominant thinking of either camp mentioned above. (I restrict this discussion to interspecific interactions, although positive and negative intraspecific interactions have almost certainly played a role in the macroevolutionary dynamics of some clades. I also will not discuss community-level effects of biotic interactions, or the substantial macroevolutionary role of interspecific hybridization.) I start with three basic areas in which the lack of integration hinders understanding, outline three apparent contradictions between short- and long-term datasets, and conclude with several promising foci for integrated analysis, with examples involving each major interaction type: competition, predation, mutualism, and commensalism/amensalism.

Problem 1: Scale and Hierarchy Matter

The macroevolutionary role of interspecific interactions has been discussed since Darwin (1859), but generally with little attention to scale and hierarchy. The short-term, local interactions most readily dissected by close observation and experiment can vary in intensity or even sign at different spatial scales (e.g., Englund and Cooper 2003; Leibold et al. 2004; Hoopes et al. 2005; Thompson 2005). Temporal scale can also be important: climatic and other physical events, which clearly reach high amplitudes on centennial, millennial and longer scales, can radically restructure or terminate interactions that appear stable on annual or decadal scales (e.g., Jackson and Williams 2004). Interacting species differ in their genetic population structures, which could impose different spatial and temporal scales of local adaptation, and those interacting species often have different geographic ranges, so that every species interacts with a different suite of species at different

sites over its entire range (Thompson 2005). Interspecific variation in geographic range in turn imposes differential speciation and extinction probabilities (Purvis et al. 2000, 2005; Jablonski and Roy 2003; Gavrillets 2004; Jablonski 2005a), so that different clades will drop out of interactions or donate new participants at different rates. If clades differ not just in speciation rate but in speciation mode (e.g., if plant speciation draws heavily on “instant” polyploidy, phytophagous insects on ecological speciation, and mammalian herbivores on classic allopatric speciation), then the temporal and spatial scales of these events, and their adjustment to local biotic and abiotic environments, will vary significantly among interactors on evolutionary timescales (see Howard and Berlocher 1998; Coyne and Orr 2004; Dieckmann et al. 2004; Gavrillets 2004).

Even less explored is how the hierarchical structure of biological systems—organisms within demes within species within clades—can confound simple extrapolation (for a range of hierarchical approaches to evolution, see Valentine 1973, 2004; Stanley 1979; Eldredge 1985; Williams 1992; Jablonski 2000, 2007; Gould 2002; Okasha 2006). Events at the organismic level—shifts in abundance or in birth and death rates—need not impinge predictably on dynamics at higher levels. Thus, antagonistic interactions such as competition or predation, which by definition have negative fitness effects on one or more participants at the organismic level, can evidently increase or decrease speciation rates, and positive, mutualistic interactions can evidently increase or decrease extinction probabilities at the species and clade level (Table 1). At the same time, higher-level dynamics—shifts in taxonomic or phenotypic diversity or in origination and extinction rates of apparently interacting clades—need not correspond in any simple way to lower-level processes. Not only can temporally concordant or reciprocal diversification dynamics represent independent responses to an additional physical or biotic factor (in a macroevolutionary analog to apparent competition and apparent mutualism), but, as in any hierarchical system, high-level patterns can potentially be underlain by more than one process at the lower (organismic or species) level. Without additional information, for example, an increase in the species-richness of a thick-shelled molluscan clade might be driven by factors ranging from organismic selection via predation, to hitchhiking on speciation-promoting factors such as low larval dispersal rates, to changes in climate or ocean chemistry.

This lack of a one-to-one mapping across levels is of course no reason to disregard either organismic or clade-level patterns. Predictions from short-term local observations are respectable seeds for a macroevolutionary hypothesis. They should, however, be hypotheses and not assumptions. Clearly the way forward is a multilevel approach (e.g., Jablonski and Hunt 2006), with formal comparative analysis to factor out confounding covariation. However, neither present-day ecological data nor diversity histories are

Table 1. Qualitative classification of interactions according to their net effect on organismic fitness (+, −, or 0, after Bronstein 2001), and on two clades whose species are interacting (in terms of origination rates [O] and extinction rates [E]). This table is not exhaustive, but aims at posing the question: When do the interactions translate into congruent effects at the level of clade dynamics?

Organismic interaction	Organismic fitness effects	Clade-level effects	Clade-level references
1. Competition	−, −	−, −	MacArthur 1972; Stanley 1973, 1979, 1985 (high E); Maurer 1989 (low O); Matsuda and Abrams 1994a; Miller and Sepkoski 1988; Sepkoski 1996; Dieckmann and Doebeli 2004 (high E); Pfennig and Pfennig 2005
		+, +	Stanley 1973, 1979, 1985 (high O); Bagnoli and Bezzi 1997; Schluter 2000a; Dieckmann and Doebeli 2004 (high O); Vamosi et al. 2006
2. Predation/herbivory	+, −	+, −	MacArthur 1972; Stanley 1985, 2007, 2008 (high E); Matsuda and Abrams 1994b; Blackburn et al. 2005; Holt and Hoopes 2005; Vamosi 2005; Mayhew 2007; Smith and Benkman 2007; Sax et al. 2007; Seehausen 2007; Vellend et al. 2007
		+, +	Stanley 1985, 1986, 1990, 2007, 2008 (high O); Schluter 2000a; Rundle et al. 2003; Dieckmann and Doebeli 2004 (high O); Vamosi 2005; Nosil and Crespi 2006; Langerhans 2007; Langerhans et al. 2007; Meyer and Kassen 2007
		−, −	Rosenzweig 1977; Stork and Lyal 1993; Koh et al. 2004; Van Valkenburgh et al. 2004
3. Parasitism	+, −	+, −	Boots and Sasaki 2001, 2003; Vinogradov 2004; de Castro and Bolker 2005; Smith et al. 2006
		+, +	Thompson 1987; Werren 1998; Hurst and Werren 2001; Buckling and Rainey 2002 (among but not within host populations); Summers et al. 2003; Bordenstein and Werren 2007; Mayhew 2007; Seilacher et al. 2007
		−, −	Webb 2003
3. Amensalism	0, −	0, −	Thayer 1983; Bottjer et al. 2000; Odling-Smee et al. 2003; Dornbos 2006
		0, +	Bottjer et al. 2000; Dornbos 2006; Marengo and Bottjer 2007
4. Mutualism	+, +	+, +	Levin 2000; Coyne and Orr 2004; Thompson 2005; Johnson 2006; Kay et al. 2006; Gegar and Burns 2007
		−, −	Koh et al. 2004; Webb 2003; Kiessling and Baron-Szabo 2004; Sachs and Simms 2006
5. Commensalism	0, +	0, +	Odling-Smee et al. 2003; Alfaro et al. 2007; Johnson et al. 2007
		0, −	Koh et al. 2004

sufficient to demonstrate macroevolutionary consequences for biotic interactions (although those data can often falsify causal hypotheses, see below). Subsidiary data are needed, including two severely underutilized paleobiological approaches discussed below: (1) use of natural experiments tracking dynamics of focal clades through a key time interval in the presence and absence of hypothesized interactors, and (2) critical analysis of functional data on the interactive capability of clades that may change their functional properties over time.

Problem 2: Respective Weaknesses of Neontological and Paleontological Data

The multidisciplinary approach will be most powerful with the integration of paleontological and neontological data. Each type

has its shortcomings. For example, strictly neontological data often cannot constrain past spatial distributions (examples are legion, but see the oldest known hummingbird, an exclusively New World clade today, in the Eocene of Germany; Mayr 2004), congruent tree topologies need not signal synchronous branching events (e.g., Brooks and McLennan 1991; Percy et al. 2004; de Queiroz 2005; Lopez-Vaamonde et al. 2006; Smith et al. 2007), and observed diversities are net outcomes of origination and extinction that are difficult to break apart without prohibitively large data arrays and restrictive model assumptions (e.g., Paradis 2004; Ricklefs 2007 and references therein). Neontological time frames cannot encompass the full range of biotic and abiotic factors encountered over the history of target clades, and are limited in the phenotypic histories recorded for natural populations. We still do not understand how a chain of ecological moments translates into long-term evolutionary trajectories: evolution can be

amazingly quick in the wild and in the laboratory, but the fossil record shows that much of that short-term responsiveness turns out to be oscillatory and bounded, with net changes tending to accrue more episodically (e.g., Jackson and Cheetham 1999; Gould 2002; Eldredge et al. 2005; Hunt 2007a). Despite some progress linking “lines of least evolutionary resistance” to longer-term dynamics (cf. Schluter 1996, 2000a; Hunt 2007b; but see Renaud et al. 2006), short-term data are surpassingly difficult to project reliably to macroevolutionary outcomes.

On the other hand, paleontological data only address restricted sets of organisms (mostly those with geologically durable remains), provide limited sets of characters for analysis, sample a narrower range of habitats and regions than living taxa, and are not amenable to direct behavioral observations (with some exceptions noted below) or experimental manipulation (NRC 2005). Further, the temporal resolution of paleontological data rarely permits detailed tracking of populations on annual, decadal, or centennial timescales. Time-averaging of biotic assemblages—the mixing of remains before final burial—can collapse the ecological record within a sample to decadal, centennial, or coarser resolution, although mounting data suggest that the majority of material in most marine skeletal samples comprise decadal to centennial timeframes, and macroscopic plant assemblages appear to be genuine ecological snapshots (Kidwell and Flessa 1995; Martin 1999; Kidwell 2002; NRC 2005). Temporal correlation among localities is generally coarser, although geological dating techniques are advancing at a pace where patchy sampling and sedimentary deposition may become the limiting factor to temporal resolution (Kowalewski and Bambach 2003; Erwin 2006).

A major challenge to macroevolutionary analysis is the strong asymmetry in the preservation potential of many sets of interactors. Predators tend to be significantly rarer than prey and so more likely to be undersampled, but more importantly, skeletonized marine prey and woody or well-cuticularized plants have much richer fossil records than many of their respective enemies (marine fish, crabs, seastars and terrestrial insects; not to mention their nematodes and other parasites). Conversely, only a subset of skeletonized predators consume equally preservable prey; for example the most diverse molluscan carnivores (turroid gastropods including the cone shells) prey mainly on soft-bodied benthos.

This (abbreviated) list of shortcomings drives home the point that both neontological and paleontological data are incomplete and are far more powerful when used in tandem. This linkage will require thought about research strategies. For example, although paleontological data can rarely trace the generation-by-generation response of one species to another, they provide unique temporal sequences of clade-level trends

in morphology and abundance, and such key macroevolutionary variables as origination, extinction, and spatial shifts.

Problem 3: The Several Currencies of Macroevolution

A battery of simplifying assumptions have been used to analyze macroevolutionary dynamics in an ecological context. Many are justifiable for broad-scale analyses, but all deserve scrutiny as improved data and theory become available and as the focus narrows. Two deserve special mention because they cut directly to the kinds of data being analyzed, and dissecting each case is sure to yield novel insights.

First is the assumption that taxonomic, morphologic, and functional variety correlate in a simple fashion. These different aspects of biodiversity do tend to covary in a coarse way: species-poor clades or assemblages above the present-day Arctic Circle generally comprise less overall morphological and functional diversity than, for example, the species-rich clades or assemblages of the present-day tropics. In this sense, the frequent use of taxonomic diversity (often at higher taxonomic levels) as a proxy for morphological or functional variety is reasonable. However, discordances between taxonomic and morphological variety—often measured within a multivariate morphological space (morphospace) and termed disparity—are well known and highly informative. Most famous is the rapid expansion of morphospace occupation, relative to taxonomic diversification, during the early Paleozoic explosion of marine animal life, the mid-Paleozoic invasion of land by plants and animals, and several other major radiations (for reviews see Foote 1997; Erwin 2007; Jablonski 2007). These episodes are taken to indicate that clades tend to occupy morphospace rapidly relative to their species- or genus-level diversification rate when presented with relatively open ecological landscapes, and that the two metrics become more tightly correlated in more “crowded” settings (e.g., Walker and Valentine 1984; Valentine 1990; DiMichele et al. 2001; Jablonski et al. 2003a). More work is needed on how this works within individual clades, and on how relationships between taxonomic and morphological diversity, and between morphological and functional variety, tend to break down temporally and geographically at finer scales (e.g., Roy et al. 2004; Alfaro et al. 2005; Wainwright et al. 2005; Young et al. 2007). The discordances among macroevolutionary currencies do not necessarily negate the largest-scale work on paleobiologic patterns, and the use of higher taxa as crude proxies for disparity has been validated repeatedly (reviews by Erwin 2007; Jablonski 2007), but treating the different variables independently will undoubtedly yield new insights.

Second is the assumption of a simple correlation between species richness and relative abundance of clades. Most

macroevolutionary analyses, whether neontological interclade comparisons or paleontological tracking of clade dynamics, focus on variations in taxonomic richness. The frequent assumption that these variations roughly reflect changes in abundance is obviously risky but has largely been applied judiciously (and out of necessity): major diversifications in the fossil record probably do tend to signal an increase in ecological importance, for example, particularly given that exceedingly rare taxa generally do not contribute to observed fossil diversity (see Novack-Gottshall and Miller 2003 for a thoughtful discussion and analysis of early Paleozoic molluscs; also Bambach 1993; Huntley and Kowalewski 2007). However, more detailed analyses incorporating abundance data have begun to detect interesting discordances between clade abundance and diversity. For example, in the marine bryozoan clade Cheilostomata, global genus diversity, local species richness, and local abundance track one another fairly well from their Early Cretaceous origin to the present day. However, this covariation breaks down in the related clade Cyclostomata following the end-Cretaceous extinction (65-Myr ago), with nearly constant local diversity (although with high variance) and significantly declining local abundance through the Cenozoic (McKinney et al. 1998, 2001).

Analyses of clade dynamics related to these two variables will be promoted by online databases that include local abundances (e.g., the Paleobiology Database), given growing evidence that rank abundance data are, at least for some groups, robust to the vagaries of fossilization (Kidwell 2001, 2007; Jackson and Williams 2004; Jackson and Booth 2007). One intriguing result is that the shape of species-abundance distributions in marine communities changed significantly from the Paleozoic to the post-Paleozoic (Wagner et al. 2006), implying a substantial reorganization in ecological structure as the biota rediversified from the massive end-Paleozoic extinction. The early Paleozoic decline in trilobite abundance relative to other benthic groups, despite only minor changes in genus richness, also demonstrates decoupling of ecological structure from taxonomic metrics (Finnegan and Droser 2005); comparable discordances occur in terrestrial plants (Wing and Boucher 1998; Lupia et al. 1999; Schneider et al. 2004; Boyce et al. 2007).

Apparent Contradictions across Scales

A number of biotic patterns have emerged over the past few decades that challenge assumptions on simple relationships between short- and long-term roles for biotic interactions, for example on the scaling up of competition or predation experiments to among-clade differences in speciation and extinction rates. These discordances are becoming increasingly well known, but they are still not consistently incorporated in research design or interpreta-

tion, and their macroevolutionary implications have barely begun to be explored. Three representative problems in reconciling observations at different scales are discussed below.

How to reconcile the individualistic geographic shifts of species on centennial and millennial timescales with fine-tuned coevolutionary relationships? Such shifts are well documented in temperate terrestrial and marine systems (Valentine and Jablonski 1993; Jackson and Overpeck 2000; Watkinson and Gill 2002; Lyons 2003; Jackson 2004; Jackson and Williams 2004; Lovejoy and Hannah 2005). However, we still know little about range shifts in the tropics, where many of the most striking mutualistic and parasitic relationships reside, although the few available data suggest individualistic behavior there too (Colinvaux and De 2001; Bush et al. 2004; Mayle et al. 2004). Failure to reject a null hypothesis of total independence for Pleistocene species movements has occasionally been held to validate claims for “community unity” over these timescales (e.g., McGill et al. 2005; Jackson and Erwin 2006; but note that McGill et al. find shuffling of species associations to be greater than expected by chance). However, species with similar climatic requirements will inevitably move in broadly similar directions during glacial–interglacial cycles even without strong biotic interactions; a null model that allows polar bears in Florida or hippos in Norway is too unrealistic to be meaningful (Jackson and Overpeck 2000; Jackson 2004; Graham 2005; Lyons 2005). Further, independent movement of species having overlapping distributions is detectable only at the edges of their respective geographic ranges, which are rarely sampled paleontologically, particularly in terrestrial systems (Roy 2001) (Fig. 1). Thus, apparent temporal stability in fossil assemblages could readily be a passive consequence of sampling, overlapping tolerances, and displacement rates. Individualistic behavior does not exclude coincident shifts or geographic ranges among species, but the mechanisms and expected consequences differ from those of a “community unity” model.

Individualistic behavior does not imply the absence of biotic interactions: plants must still be pollinated, herbivores must still find suitable plants, carnivores must still subdue prey, and the lack of repeated waves of Pleistocene extinction suggests that in fact they managed to do just that on land and in the sea (e.g., Valentine and Jablonski 1993; Coope 1995, 2004; Jackson 2004). But how to reconcile the spatial volatility of species distributions with the evolutionary dynamics of sets of closely associated species, such as flower and pollinator or host and parasite? One possibility is that (1) close associations observed today represent the subset of cooccurring species that either happened to move in concert owing to shared climatic and other requirements, or moved independently but maintained at least partial range overlap (e.g., Thompson 2005; and see DeChaine and Martin [2006] for a striking comparative phylogeographic analysis). Alternatively, (2) pairwise species relationships represent rapid adjustments (on the

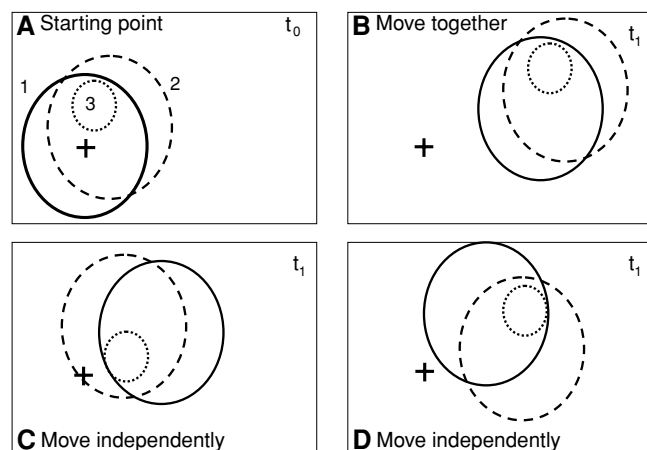


Figure 1. Shifting geographic ranges of three species; cross is initial position of centroid for species 1, for reference. (A) Starting point for three species that share similar abiotic environmental requirements. (B) All move together. (C, D) The three species move independently. In all of these scenarios, species 3 remains fully embedded within the geographic ranges of species 1 and 2, and species 1 and 2 remain overlapping by more than 50% of their geographic ranges (i.e., range centroids still fall within the other species' ranges). Thus, individualistic versus coordinated movement can only be detected paleontologically in areas of former overlap or former vacancy now occupied by only one species; simple, prolonged coevolution is more likely between species 3 and the other two species, but coevolution in a geographic mosaic is feasible between species 1 and 2. Inspired by Roy (2001), for a niche-based version of this figure, see Jackson and Williams (2004).

order of 10^2 – 10^3 yrs) that permit “ecological fitting” into complex relationships even without long-term association (Janzen 1985), perhaps layered on top of more diffuse coevolution involving, say, broader clade-level interactions that might persist even as particular species kaleidoscope past. The rapid evolution repeatedly seen in native species as they ecologically fit to exotics (Sax et al. 2007) argues against any need for a deep phylogenetic history of association. Many specialized systems may show deep phylogenetic congruence, with codiversification of higher taxa dating back tens of million of years, but considerable host-switching at the species level (e.g., Cook and Rasplus 2003; Currie et al. 2003; Rønsted et al. 2005), as might be expected in the face of extensive secular environmental change and ~ 20 Pleistocene climate cycles. Combined paleo- and neoanalyses of the few sets of interacting species having similar preservation potential (certain phytophagous beetles and their host plants, for example) are needed to determine how and when short-term observations can be matched to protracted ecological and evolutionary associations. The independent spatial shifts that undermine attempts to infer speciation modes from modern distributions (see Losos and Glor 2003; Gavrillets 2004, p. 206) are also obstacles to inferring deep coevolutionary histories from modern associations.

Clearly, individualistic range shifts can sometimes outpace even the most nimble coevolvers, as seen today as climate changes create mismatches between predators and prey, pests and controls, hatchlings and critical resources (e.g., Bradshaw and Holzapfel 2006; Parmesan 2006). The evolutionary formation and disassembly of close ecological relationships is thus not just a theoretical issue. Contrasting biologies must amplify such mismatches over broader timescales, and it is remarkable that so little has been done comparing the evolutionary responses of annual plants or short-lived rodents (or snails or sea urchins) to those of long-lived trees or clonal reef corals that may have been through only a few dozen generations (as measured by genetic individuals) since the last ice age (Potts 1984). And probing slightly deeper into the evolutionary roots of biotic associations, several authors have suggested that the lengthy cooccurrences expected during more equable past climates should produce richer and deeper biotic partnerships than seen for clades that only came into contact during times of high-amplitude climate changes (DiMichele et al. 2004). Similarly, regions in which accidents of geography have damped the amplitude of climate swings, as suggested for the Cape Province of southern Africa, might be expected to harbor more intense or complex biotic relationships than areas at similar latitudes but greater climatic volatility (see Jansson 2003).

How to reconcile the fact that species are embedded in extensive and dynamic networks of interactions with the evolution of costly enemy-specific defenses and finely attuned mutualisms? The classical approach to biotic interactions focuses on pairwise interactions, if only for tractability. However, it is increasingly clear that networks of interacting species are generally the rule, and that these interactions are spatially more complex than previously thought (e.g., Janzen 1980; Rausher 1996, 2001; Stanton 2003; Thompson 2005; Bronstein et al. 2006; Waser and Ollerton 2006). Even many examples of supposed obligate species pairs, as in figs and fig wasps, have proven to involve suites of species, with multiple pollinators per host and multiple hosts per pollinator (Machado et al. 2005; Haine et al. 2006; Erasmus et al. 2007; Marussich and Machado 2007; but see Weiblen 2004 on morphological sorting). The concept of “diffuse coevolution” has been applied too broadly, as Thompson (2005) notes, and a simple dichotomy between pairwise and “diffuse” interactions is just the first step toward understanding processes. However, promising developments toward gaining a more integrative macroevolutionary perspective include the development of protocols for more rigorous treatment of diffuse interactions (see Rausher 1996; Iwao and Rausher 1997; Strauss et al. 2005; and reviews by Agrawal et al. 2006; Johnson and Stinchcombe 2007), and the growth of theory and data bearing on a geographic mosaic of coevolution, directly incorporating spatial and temporal variation in the intensity and sign of multiple interactions (see Thompson 2005; Gomulkiewicz et al. 2007).

Is the conceptual tension between the transience of most ecological associations and the apparent pervasiveness of evolutionary accommodation and antagonism among species fully resolved by coevolutionary theories founded on diffuse interactions or geographic mosaics? Ecological communities at any one time and place tend to skew toward a few strong and many weak interactions (Wootton and Emmerson 2005), which may reduce the challenge for theory and models, but translation of short-term observations on geographic mosaics, interaction networks, and skew in interaction strengths, to macroevolutionary outcomes through time and across clades remains poorly constrained.

At least some of the newer approaches to coevolution aim explicitly toward addressing the failure of local coevolution to extrapolate to longer timeframes (e.g., Thompson 2005), but we still need to know whether spatial and among-clade variations in the topology of species interactions within networks impose predictable, first-order controls on the fates of species and the long-term shaping of phenotypes. One direction is suggested by evidence that antagonistic networks (herbivore-plant, predator-prey) tend to be more modular or compartmentalized (Holt 1995; Holt and Hoopes 2005), whereas mutualistic networks tend to be more nested with generalists interacting with each other and specialists interacting only with generalists (e.g., Thompson 2005; Guimarães et al. 2006; Lewisoyn et al. 2006; Waser and Ollerton 2006; Ollerton et al. 2007; antagonistic symbionts may also tend toward nested distributions, see Rohde et al. 1998). These structures could translate into macroevolutionary dynamics if nested structures are indeed more resistant to environmental perturbation and extinction than modular ones (e.g., Memmott et al. 2004; Jordano et al. 2006; Ollerton et al. 2007), and nestedness varies with species richness (either for mathematical or biological reasons, see Guimarães et al. 2006). Most interaction modules could be short-lived, for example, with the participants repeatedly finding new partners in time and space so that just a few of the myriad local coevolutionary experiments have any significant duration (Thompson 2005). But a deeper-time and spatially explicit window is needed to test this attractive hypothesis in macroevolutionary terms. Amazingly, virtually nothing has been done to integrate the rich, spatially detailed Quaternary fossil record of plants (Jackson and Williams 2004 and others cited above) with the equally rich record of Quaternary insects (Elias 1994; Coope 1995, 2004). A few anecdotes suggest that phytophagous insects have detached from and rejoined their putative host plants over time (Coope 1995), but the evolutionary implications of these sparse observations have not been explored.

How to reconcile rapid microevolution of advantageous phenotypes, and the invasibility of most communities, with the delays often seen between the origin of a clade or an evolutionary novelty and its later diversification? The delays—macroevolutionary lags—often seen between the time a novelty appears and the diver-

sification or rise to ecological prominence of the clade it defines (e.g., calcareous algae, mammals, and angiosperms) have several potential explanations (Jablonski and Bottjer 1990). When the null model of simple exponential growth can be ruled out (as Patzkowsky 1995 did for mammals and bryozoans), a macroevolutionary role of antagonistic biotic interactions must be considered, as most famously held for the long Mesozoic lag and exuberant Cenozoic diversification of mammals after the extinction of nonavian dinosaurs and several other dominant terrestrial, marine, and aerial vertebrate clades. Such discordances can also be seen in comparisons among the macroevolutionary currencies. For example, clades might theoretically reach ecological dominance prior to diversification, but abundance more frequently appears to lag behind diversity, as in the 10-Myr gaps between taxonomic diversification and increase in abundance among angiosperms (Lupia et al. 1999) and among North American grasses (Strömberg 2005).

Incumbency or priority effects, where one clade excludes or hinders another owing not to competitive superiority but to historical contingency (colonization or origination sequence) (e.g., Case 1991; Almany 2003; Fukami 2004; Irving et al. 2007; Louette and De Meester 2007), are held to underlie many macroevolutionary lags (e.g., Valentine 1980; Van Valen 1985; Rosenzweig and McCord 1991; Alroy 1996; Jablonski and Sepkoski 1996; Eldredge 1997, 2002; Jablonski 2000, 2001; Seilacher et al. 2007). As already noted, the most famous example is the Mesozoic lag and early Cenozoic diversification of the mammals (Alroy 1999 and references therein; Bininda-Emonds et al. [2007] were taken to negate an evolutionary effect of dinosaur extinction on mammals, but their molecular analysis overemphasized crown groups, see Cifelli and Gordon 2007; Wible et al. 2007). Other examples of evolutionary incumbency and its release arguably include other diversifications following major extinction events (Miller and Sepkoski 1988; Patzkowsky 1995; Foote 1997; McKinney 1998; Sepkoski 1998; Erwin 2001; Jablonski 2001) (Fig. 2); the delay in the replacement of straight-necked turtles by more derived clades (Rosenzweig and McCord 1991); the rarity of evolutionary transitions between aquatic and terrestrial ecosystems (Vermeij and Dudley 2000); the slowing of the Cambrian Explosion of marine invertebrates (Valentine 1995); and the limited number of limb-reducing lizard clades within a given region of the globe (Wiens et al. 2006). The radiation of clades on “empty” islands, such as the Galapagos finches, the Hawaiian honeycreepers, and the Hawaiian silverswords, have also been viewed as escapes from incumbency effects (e.g., Schluter 2000a). Many of these examples are plausible, but improved protocols for retrospectively—nonexperimentally—separating incumbency effects from more conventional competitive hierarchies would be valuable.

The processes actually underlying postextinction and opportunistic diversifications are poorly known. Relaxed selection at

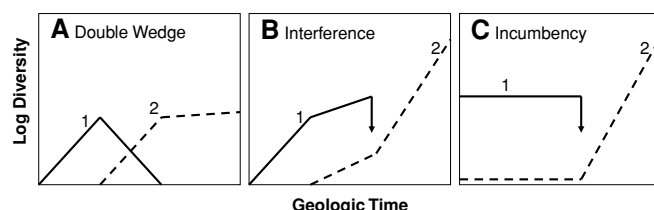


Figure 2. Three simple models of antagonistic clade interactions. (A) Double-wedge dynamic, wherein the expansion of Clade 2 drives Clade 1 to extinction; shown here under Sepkoski's (1984) logistic assumption. (B) Interference dynamic, wherein both clades reciprocally damp diversification; unimpeded diversification rate of Clade 1 seen before advent of Clade 2, unimpeded diversification rate of Clade 2 seen after extinction of Clade 1. (C) Incumbency dynamic, wherein Clade 1 precludes the diversification or introduction of Clade 2 until the extinction of Clade 1 allows Clade 2 to diversify. Similar patterns might also be expected for abundance and morphology (see for example Hopkins 2007).

the organismic level owing to newly available resources and environments has often been invoked (e.g., Simpson 1953; Valentine 1973; Schluter 2000a), as has exceptional survival of incipient species (e.g., Stanley 1979; Valentine 1980). These ideas are probably at least part of the story, but exist mainly as verbal models that are too permissive to predict, for example, why some surviving clades fail to participate in postextinction diversifications (Jablonski 2002). New quantitative models are needed that link evolving ecologies to the dynamics of surviving or invading clades (for two very different steps in this direction see Gavrillets and Vose 2005; Roopnarine et al. 2007).

The abundant evidence for a biotic component to macroevolutionary lags does seem at odds with equally abundant evidence for the invasibility of ecological communities and regional biotas in modern times, the Pleistocene, and throughout the older fossil record, especially in light of the apparent scarcity of competitive extinction in the recipient biota (e.g., Vermeij 1991, 2005a; Gurevitch and Padilla 2004; Jackson and Williams 2004; Jablonski 2005b; Jablonski et al. 2006a; Smith and Shurin 2006; Sax et al. 2007). The frequent expansion of new marine genera and higher taxa out of the tropics and from shallow to deep water both suggest a larger-scale version of the individualistic behavior of Pleistocene species (although the latter are tracking climates rather than traversing them as the large-scale patterns seem to do), in that those dynamics fuel a continually shifting species set at any one place. As with Pleistocene communities, there is no evidence that these invasions drive extinction or other major ecological disruptions; ecological associations at this large scale are evidently permeable and resilient systems (Jablonski 2005b; Jablonski et al. 2006a). However, comparable data on the movements of, for example, predatory crustaceans or fish are needed to test the limits of this resilience.

At least four nonexclusive explanations may account for the evolutionary invasibility of ecosystems: altered abiotic conditions (e.g., Strömberg 2005 on the Miocene spread of grasslands); prior removal of incumbents (e.g., Vermeij 1991, 2005a in the fossil record, Case 1996 and Morrison 2000 in the present day); undersaturation (e.g., Levine and D'Antonio 1999; Callaway and Maron 2006; Richardson and Pyšek 2006; Fridley et al. 2007); and competitively dominant invaders (often with the richer and more widespread biota exporting species "in which antipredator and competition-related adaptations have evolved to absolutely higher performance standards," e.g., Vermeij 2005b, p. 322; see also Darwin 1859; Vermeij 1978, 1991; Beard 1998; Briggs 2003; but see Valentine et al. 2008). Each alternative has support in some instances and counterexamples in others, and so all must be incorporated into a predictive theory, and each provides rich opportunities for integrative research. The biggest challenge may be to separate the expected effects of competition on macroevolutionary dynamics from other antagonistic interactions: the extinction of the dinosaurs also removed important predators on mammals and birds, the Cambrian explosion also generated predators and parasites.

Promising Research Areas: From Organismic Interactions to Clade Dynamics

COMPETITION: DOUBLE WEDGES AND COUPLED LOGISTICS

The view that organismic competition is a primary force in macroevolution has a long pedigree: Darwin (1859, p. 121) saw interacting clades as impeding not only one another's taxonomic diversification, with his famous metaphor of species wedging into a crowded space, but their occupation of morphospace (Gould 2002, p. 236). But again predation and parasitism might have similar macroevolutionary effects: damped diversification in the presence of enemies, and evolutionary bursts after extinction events that remove enemies. Conversely, the origin or invasion of a predator might promote the persistence and even the diversification of a clade previously hindered by a competitor (e.g., Stanley 2008), although such a macroevolutionary analog of predation-mediated coexistence has not been tested explicitly. Paleontological data should be able to break these conundrums, at least in principle, using combined temporal, functional, spatial, and other evidence as discussed above (e.g., Roy 1996 for two clades of stromboid gastropods). Such an approach might be applied to the trigoniid bivalves, reduced now from their Mesozoic heyday of >35 globally distributed genera and several hundred species per time bin to a single "living fossil" genus and 6 or 7 species restricted to Australian waters: were they outcompeted by functionally similar bivalves (Tashiro and Matsuda 1988), or

did their inability to burrow as deeply in the sediment as the siphon-bearing veneroids put them at a disadvantage with the Mesozoic–Cenozoic increase in predation intensity? Again, a spatially explicit analysis of the diversity and abundance history of the putative competitors and likely predators should falsify some alternatives.

For decades, the expected macroevolutionary expression of competitive interaction between clades was a simple pattern of reciprocal diversity: one clade declining while another rose in taxonomic richness, abundance, and/or disparity (Fig. 2A). With improved paleontological sampling and analysis, this classic “double wedge” pattern proved to be scarce (Benton 1987, 1996), but as Sepkoski (1996) argued, antagonistic clade interactions, whether competition, predation, or parasitism, can generate more complex coupled dynamics, perhaps most importantly as damped but positive diversification rates (Sepkoski 1984, 1996, assumed logistic functions, but clades’ diversification histories can be linked absent large-scale carrying capacities) (Figs. 2B and 3). Simple intuitive arguments for scaling up local interactions come easily: competition or predation decreases population sizes and/or intrinsic growth rates, thereby making species more vulnerable to stochastic extinction (although Vermeij [1994] explicitly rejects escalation in predation intensity as an extinction driver, on mainly theoretical grounds). Origination rates might be depressed

in the same way if biotic interactions reduce the population sizes of isolates and thus their probability of surviving to speciation (e.g., Stanley 1979, 2007, 2008). Conversely, elimination of demes within a metapopulation might isolate the others and spur speciation under some circumstances (e.g., Stanley 1986, 1990). Mathematical models and simulation studies of speciation are becoming increasingly sophisticated (e.g., Gavrillets 2004 and later papers), and inclusion of factors sensitive to the biotic and abiotic environment (genetic connectedness and spacing of subpopulations, population size, geographic range, intensity of selection for local adaptation) suggests potential for exploring the positive and negative impacts of antagonistic interactions on speciation rates, but relatively little work has been done in that direction.

One of the longest-running competitive hypotheses in paleobiology involves the articulated brachiopods and the bivalve molluscs. The brachiopods are shelled, suspension-feeding lophophorates that dominated marine shelf communities through the Paleozoic but exhibit low diversity and abundances in most habitats today. The roughly reciprocal pattern of bivalve diversification—another group of shelled, suspension-feeding invertebrates that today occupy much the same range of body sizes and marine environments—was often interpreted in terms of competitive displacement, and brachiopods today do lose to mussels where space on hard substrata is limiting (Thayer 1985). However, Gould and Calloway’s (1980) analysis found little evidence of detailed reciprocal dynamics, and saw the greater and more lasting losses suffered by the brachiopods in the huge end-Paleozoic mass extinction as the first-order driver. Sepkoski (1996) found that the dynamics of the two clades could be fitted to coupled logistic models, thus reviving a potential role for competition, but as Stanley (2008) argues, the model parameters may not be scaled realistically. On the other hand, Fraiser and Bottjer (2007) go too far in attributing both bivalve rise and brachiopod fall entirely to the end-Paleozoic event: the dominant bivalve genera in the immediate aftermath of the extinction are phylogenetically distant from those that launched the post-Paleozoic bivalve expansion, and the brachiopods did begin to rediversify in the Mesozoic along with marine bivalves (e.g., Sepkoski 1996; Walsh 1996; Greene et al. 2007). Biotic interactions probably were important in the fading of the brachiopods, but the rise of shell-crushing predators and other enemies was almost certainly a key factor (Stanley 1974, 1977, 2008; Vermeij 1977, 1987). A spatially and environmentally explicit analysis of the dynamics of the two clades during the Mesozoic, as begun by Walsh (1996), is clearly needed.

A stronger case for a protracted clade displacement in the double-wedge mode can probably be made for competitive replacement of the multituberculate mammals by rodents in the early Cenozoic (Van Valen and Sloan 1966; Krause 1986 and citations therein; also Legendre and Hartenberger 1992; Wall and Krause 1992), although, again, a role for diversifying mammalian

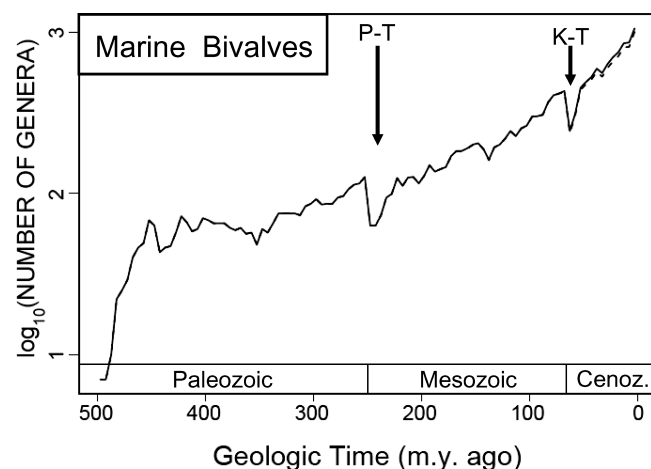


Figure 3. Marine bivalve genus diversity through time (note semi-log axes). Are the steep rebounds from the Permo-Triassic (P-T = end Paleozoic) and Cretaceous-Tertiary (K-T = end-Mesozoic) mass extinctions attributable to release from competition, release from predation, exceptional diversification owing to novel ecological opportunities, or some other ecological or preservational factor? The first two seem the most likely but fuller analysis is needed. Broken line at right of curve shows (negligible) effect of factoring out the Pull of the Recent, a potential sampling bias. The diversity plateau from ca 450 Myr to 350 Myr ago also has several potential explanations. After Jablonski et al. (2003b), inspired by Miller and Sepkoski (1988).

carnivores and raptorial birds is difficult to exclude at this point (see also Hooker 1998). This system deserves more detailed evaluation of spatial patterns, dynamics of subclades, and morphological and functional spaces occupied by the potential interactors.

Perhaps the best system for evaluating the macroevolutionary impact of competition involves encrusters of marine hard substrata. Although some key players are poorly preserved (e.g., sponges and tunicates), overgrowth patterns of skeletonized encrusters—including bryozoans, corals, bivalves, gastropods, polychaetes—offer snapshots of ecological interactions sampled on geologic timescales. The rise to dominance of cheilostome bryozoans from humble Cretaceous beginnings and the persistence of cyclostome bryozoans, often at high latitudes or as fugitives near the bottom of a competitive hierarchy, is a good case, and plays out differently in the different macroevolutionary currencies, as noted above (see also McKinney 1995; Jablonski et al. 1997; Barnes 2000, 2002; Barnes and Dick 2000; Sepkoski et al. 2000; McKinney et al. 2001; Taylor and Wilson 2003). Still lacking in these admirable analyses is the phylogenetic dissection of the Order-level patterns and how they are conditioned on the one hand by adaptations of the competitors, and on the other by evolutionary changes in the rest of the encrusting biota. For example, the rather constant 66% overgrowth success of cheilostomes over cyclostomes might represent a constrained competitive standoff, an upward-spiraling arms race within subclades, a relay of increasingly powerful subclades on both sides, or interference by other competing clades. Such analyses in the fossil record are complicated by the diffuse nature of many of the interactions under consideration, but this is a singularly promising system for neo/paleo collaboration.

At finer scales, competition has often been viewed as driving evolutionary size increases (e.g., Kingsolver and Pfennig 2004; Hone and Benton 2005). Some size increases have probably involved sexual selection or sexual competition among conspecifics, and so fall outside the purview of this article. However, the context-dependent nature of macroevolutionary size increase seriously undermines Cope's rule of evolutionary size increase as a valid generalization, and often does not support competitive interactions as the primary driver. A number of major groups fail to show pervasive size increase when a broad inventory of size trends is available (see Jablonski 1996, 1997; Moen 2006 for reviews; for a possible exception see Hone et al. 2005). Further, at least some size trends track temperature and other abiotic factors, signaling context-specific mechanisms rather than pervasive biotic drivers (e.g., Kaiho 1998; Hunt and Roy 2006; Millien et al. 2006; Schmidt et al. 2006).

More compelling evidence for a macroevolutionary role for competition, although one that opposes simple expectations from organismic fitness, comes from the renaissance in research on divergent character displacement. Such character displacement

has been proposed to promote speciation by several mechanisms, with varying degrees of theoretical or empirical support (Schluter 2000a,b, 2001a,b; Funk et al. 2006; Meyer and Kassen 2007); past spatial dynamics are again an issue, as apparent examples of ecological character displacement can be difficult to separate from divergence in allopatry followed by ecological fitting of species that most readily coexist, (e.g., Cadena 2007; Rice and Pfennig 2007). On the other hand, interspecific resource competition may reduce the strength of divergent selection and damp speciation, as also appears to have occurred with some stickleback populations (Vamosi 2003), and character displacement may push species toward extinction rather than diversification (Pfennig and Pfennig 2005). The next step will thus be to ask whether clades subject to competitive character displacement regularly exhibit significantly different dynamics in any of the macroevolutionary currencies relative to clades in which this is a less potent force. This topic has barely been explored in the subtidal marine molluscs that provide a large part of the macrofossil record; competitive interactions may be relatively unimportant for these taxa (e.g., Stanley 2007, 2008) but related species often do exhibit clear environmental separation (e.g., by bathymetry and temperature, see Carlon and Budd 2002; Rex et al. 2005).

PREDATION: ESCALATION

Predation (here including herbivory) is generally held to increase the extinction probability of prey species, and the biotic invasion literature abundantly attests to that linkage (Sax et al. 2007). However, such antagonistic interactions can also promote population differentiation of prey, and, in a smaller but growing number of studies, speciation and net diversification (Table 1), another striking mismatch between the expectation from organismic interactions and clade-level effects.

Evolutionary interactions of predators and prey need not resemble a coevolutionary arms race. Situations in which prey respond to selection imposed by classes of increasingly dangerous enemies have been termed escalation. Evolutionary escalation has been most heavily studied in the fossil record, with examples including the Cambrian diversification of marine invertebrates (e.g., Stanley 1976; Vermeij 1990; Bengtson 1994; Marshall 2006; Bambach et al. 2007); the marine-invertebrate response to the mid-Paleozoic rise of shell-crushing fish (Signor and Brett 1984; Dietl and Kelley 2001; Huntley and Kowalewski 2007); the calcareous-algal response to durophagous grazers (Steneck 1983, 1992; but see Aguirre et al. 2000); and the lake-snail response to durophagous predators in Lake Tanganyika (West and Cohen 1994, 1996; for a potentially similar case in ancient Indonesian lakes, see von Rintelen et al. 2004). The most famous case is the post-Paleozoic increase in shell-penetrating predation and in prey defenses, termed the Mesozoic Marine Revolution (MMR). The key point for the MMR is not that Paleozoic and Cenozoic clades

differ morphologically, or that younger faunas include more elaborate shells, exoskeletons, and dentitions (as expected for any increase in range or variance from a simpler ancestor), but that aspects of Cenozoic prey morphology are increasingly predation-resistant, aspects of Cenozoic predator morphology are increasingly destructive, and direct measures of predation intensity increase in the Cenozoic, relative to Paleozoic forms (Vermeij 1977, 1987, 1994; see also Stanley 1977; Morris and Taylor 2000; Dietl and Kelley 2002; Walker and Brett 2002; Blake and Hagdorn 2003, p. 33; Harper 2003, 2006; Huntley and Kowalewski 2007). I will make four points about the MMR that apply to most large-scale antagonistic interactions.

First, the MMR was highly polyphyletic, and we lack a robust spatial and temporal inventory of the initial appearance of predator abilities, as might drive an evolutionary ratchet in prey defenses. Because functional transitions often do not correspond to the origins of higher taxa, there are rich opportunities for the tracking of biomechanical capabilities of predators and prey over evolutionary time, globally and within clades. Further, both predator and prey must be subject to trade-offs that block infinite evolutionary escalation, and these limits must be hit at different points on an absolute defensive or aggressive scale in different clades (Taylor 2001; Thompson 2005), implying that different taxa must drop out of the leading edge of the escalation process and seek different prey or different kinds of shelter at different times. Our understanding of such limits and their macroevolutionary consequences is sketchy at best, although the retreat of clades to offshore or high-latitude positions might be examined in this light (e.g., Vermeij 1987; Jablonski and Bottjer 1990, 1991; Jablonski 2005b). Preservation and other obstacles are not trivial, and damage traceable to predators may not be a good proxy of overall predation intensity; for example, analyses of drillholes generated by predatory gastropods massively dominate paleontological analyses of marine predation but represent a (spatially varying) fraction of the predation confronting prey species. Nonetheless, paleontologists have made significant strides by working at relatively coarse timescales where individual time bins capture rare occurrences of well-preserved predators, and taking advantage of the full inventory of predation traces (=fossil behavior) on the remains of the prey (e.g., Vermeij 1987; Labandeira 2002, 2007; Harper 2003, 2006; Huntley and Kowalewski 2007).

Second, escalation in the morphology of predators and prey has evidently occurred via sorting at multiple levels. As already noted, marine invertebrate species tend to exhibit morphological stasis in the fossil record, that is, nondirectional shifts within fairly narrow limits, and escalatory traits appear to be no exception. Only a few examples exhibit gradual escalation within an evolutionary lineage (e.g., Dietl et al. 2000 in the Late Cretaceous, but involving a stepwise multispecies trend; Kelley 1989, 1991, and Kelley and Hansen 2001, but in Miocene settings thought to postdate the

major rise in predation intensity). Differential survival and proliferation of more escalated species within clades, and of clades within broader assemblages of species, thus evidently contribute to escalation patterns, so that intrinsic traits and abiotic events can also shape long-term trends—escalatory traits may hitchhike on features such as genetic population structure or geographic range size (strong subdivision being positively related to speciation probability, broad range being inversely related to extinction probability; Jablonski 2000, 2007; Gavrillets 2004). These higher-level sorting processes have also been poorly documented (but see Roy 1996; Miller 1998). Conversely, more escalated prey might have greater energy demands and so be more extinction-prone (Vermeij 1987, 1999), but the most extensive tests of this hypothesis have yielded negative or ambiguous results (Hansen et al. 1999 and Reinhold and Kelley 2005; new approaches directly accessing growth rates should be more fully explored, see Dietl et al. 2002). Spatially explicit hierarchical analyses of morphological and taxonomic changes in escalating clades are sorely needed, as a simple extrapolational view is clearly inadequate here.

Third, the MMR has largely proceeded not as a set of directional trends at the clade level, but more often as what Gould (2002) termed an increase in variance. Expansion in the range of defensive or aggressive armaments within clades has evidently been the rule, with less well-armed predators tending to predominate in high-latitudes and deep-water environments, and less well-defended prey tending to persist or move there over time (Vermeij 1987; McNamara 1990; Aberhan et al. 2006). However, even in the tropics some clades retain the plesiomorphic state, and we need to understand the dynamics beyond this persistence of the trailing edge of the variation in predators and prey; morphological patterns and interaction outcomes at high latitudes seem not to represent a simple random draw of low species numbers from the larger tropical pool, but this deserves formal investigation (extending, for example, Abele et al. 1981). Comparative dissections of clade histories thus would be valuable (these biogeographic and phylogenetic considerations, along with the differential preservation potential of predators and prey and the noncorrespondence of biomechanical ability and taxonomy noted above, severely compromise the global taxonomic analyses of Madin et al. 2006; see also Aberhan et al. 2006; Bush et al. 2007).

Fourth, as the MMR hypothesis acquires (legitimate) elaborations and complications, it becomes increasingly difficult to test definitively within a given system, in part because failure to meet simple expectations can readily be accounted for in biologically plausible terms. Remarkably little theory is available on how multispecies predator–prey systems respond on long timescales to additions of, and changes in the capabilities of, participants, or how trade-offs affect evolutionary trajectories (but see Abrams 1990, 1996, 2000a,b, 2001). Some models and data suggest that the interplay between antagonistic interactions and population density

might lead not to reciprocal arms races or escalation but to stasis or even “evolutionary disarmament” (Abrams 2000b; Kisdi and Geritz 2001), particularly in the face of conflicting selection pressures (Mikolajewski et al. 2006; Zimmerman 2007). Alternative dynamics in response to antagonistic interactions have been less explored on macroevolutionary scales (e.g., fluctuating polymorphisms and “coevolutionary alternation,” see Thompson 2005; Nuismer and Thompson 2006). Imaginative approaches that blend modeling, experiment, and backtracking of evolutionary histories of extant clades into the fossil record may be needed to improve our understanding of when and how escalation has operated, in the MMR and elsewhere.

Terrestrial insect–plant systems resemble the marine predator–prey MMR in several ways. Plants evidently faced a similarly protracted and episodic onslaught from herbivorous insects, although most of the major mouthpart types had evolved prior to the origin of the angiosperms (Labandeira 1997, 2002); the most intense and diverse predation tends to occur in the tropics (Pennings and Silliman 2005; Schemske 2008); and differential proliferation of clades has clearly also occurred with derived clades better defended than basal ones (e.g., Agrawal 2007). Plants and their enemies may show greater concordance between their phylogenies—hardly a surprise in this system, where the prey often constitutes the habitat of the predator. As already noted, however, concordance of phylogeny need not indicate pairwise coevolution or cospeciation: diversification of prey can significantly precede diversification of the predator (as in Percy et al. 2004; Lopez-Vaamonde et al. 2006; but see Becerra 2003 for “roughly synchronous” diversifications). This concordance is consistent with Thompson’s (1989, 2005) formalization of the classic “escape and radiate” model (Ehrlich and Raven 1964), but phylogenetic tests have been few and results are contradictory or weak (see Agrawal 2007; and Vamosi’s 2005:905 critique of Farrell et al.’s classic 1991 study of latex-bearing plants). Direct historical data should be brought to bear on these questions, for example, paleontological evidence that the advent of latex production brought both diversification and decreased herbivore damage.

MUTUALISM: ENDOSYMBIOSES

Mutualisms are rich in potential macroevolutionary consequences, but have been neglected from this standpoint. As in other interactions, they can affect clade dynamics by altering genetic population structures, geographic ranges, and niche dimensions of one or more participants, and in extreme instances they create novel functional units and so are a pathway to major evolutionary transitions. Modeling and empirical surveys show that obligate one-to-one species pairing is rare, and most mutualisms tend toward a nested pattern, either where both partners are actually mutualistic with large numbers of species, or where one species is a specialist but the other cooperates with many species (e.g.,

Thompson 2005; Bronstein et al. 2006; Waser and Ollerton 2006; Ollerton et al. 2007). This nestedness alone should make most mutualisms capable of surviving cheaters and resistant to the demise of one or more partners (Bronstein et al. 2004; Sachs and Simms 2006). When mutualisms relate to reproduction, as in pollination systems, specialization by either partner is generally expected to increase speciation probability in the partner whose reproduction is acted upon (e.g., Johnson 2006; Kay et al. 2006). Conversely, conspecific plant populations in different environments may come under selection to adapt to different pollinators, which appears to have promoted speciation in *Mimulus* (Schemske and Bradshaw 1999) and may be important in many plants (Coyne and Orr 2004; Thompson 2005). When mutualisms relate to competitive ability or to niche breadth, as in many facilitative symbioses, we generally expect either effect to lower extinction probability of the partner: witness the mutualism that gave rise to the astoundingly successful termites (Abe et al. 2000), or the partnership between mycorrhizal fungi and plants, which was almost certainly an important factor in the colonization of land (e.g., Remy et al. 1994). However, certain obligate symbioses simultaneously enhance competitive ability and narrow niche dimensions, and such relationships may set up conflicts between short- and long-term evolutionary dynamics.

The most obvious system for evaluating the long-term risks of obligate mutualisms is zooxanthellate scleractinian corals. These photosymbiont-bearing, skeletonized cnidarians can be spectacularly abundant in their preferred habitats, but are restricted to clear, nutrient-poor, tropical marine settings at shallow depths (usually < 50 m) (e.g., Wood 1999). As predicted, zooxanthellate corals show significantly greater extinction intensities during the end-Cretaceous mass extinction than do symbiont-free corals (Rosen 2000; Kiessling and Baron-Szabo 2004) (Fig. 4). These differences do not hinge on membership in reef communities per se—extinction intensities are indistinguishable among reef, coastal, and outer shelf environments (Kiessling and Baron-Szabo 2004). We know far less about differences in extinction rates among zooxanthellate and azooxanthellate corals away from the major mass extinctions, or differences in origination rates in general. Such analyses are hampered by difficulties in matching morphological units onto genealogical ones (but see Klaus et al. 2007 and references therein for encouraging progress). Similar difficulties and opportunities abound in several clades of photosymbiont-bearing foraminifera, shelled protozoans with a rich fossil record (Norris 1996, Hallock 1999); perhaps better known if less abundant are the zooxanthellate bivalves of modern seas (Tridacninae) and the geologic past (as hypothesized for Permian alatoconchids, and the wonderfully strange and diverse Jurassic-Cretaceous rudists; see Seilacher 1990; Jablonski 1996b; Isozaki 2006).

Chemosymbiont-bearing bivalves also seem promising for analyses of the macroevolutionary impact of mutualisms, with

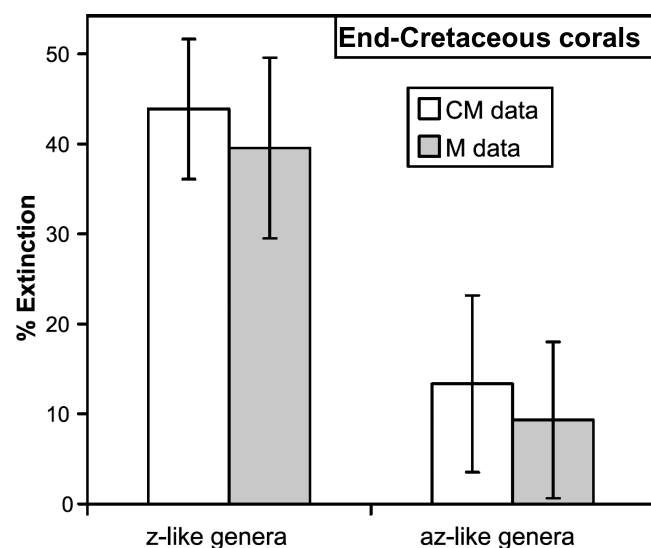


Figure 4. The macroevolutionary downside of mutualism. The end-Cretaceous mass extinction was more severe among corals apparently containing photosymbiotic zooxanthellae (z-like genera) than in azooxanthellate corals (az-like genera), whether data combine the last two stratigraphic stages of the late Cretaceous (CM data) or are restricted to data confirmed to be from the latest, Maastrichtian, stage (M data). From Kiessling and Baron-Szabo (2004), used by permission.

the lucinid bivalves perhaps the best target because they are abundant and accessible today and have a rich fossil record, with distinctive shell morphologies in symbiont-bearing species (Taylor and Glover 2000). Chemosynthetic mutualisms freed deep-sea metazoans from reliance on surface-water productivity and clearly spurred molluscan diversification around hot vents and cold seeps, complete with apparent cospeciation of chemosymbionts and their hosts (Peck et al. 1998), but the vent/seep fossil record is patchy and preservation is highly uneven (but see Kiel and Little 2006 for encouraging signs).

The outlines of a general theory of interspecific mutualism are beginning to emerge. This work is (not inappropriately) focused on cost-benefit ratios at the organismic level, but the most successful approaches have a strong spatial component (e.g., Doebeli and Knowlton 1998; Thompson 2005; Foster and Wenseleers 2006 and references therein), which suggests potential feedbacks to and from higher levels. For example, genetically subdivided or narrowly distributed species, where local conspecifics are likely to be closely related, have significantly greater scope for the evolution and maintenance of mutualisms than species where local relatedness is low (Foster and Wenseleers 2006; see also Frank 1994; West et al. 2002). Whether this hypothesis holds over the long term is testable in the fossil record of some clades, and conversely it would also be very interesting to test whether independent paleontological evidence of a clade's acquisition of an obligate mutualism coincides with changes in the spatial distribution

and evolutionary dynamics of its species. If changes in genetic population structure can increase a clade's propensity for establishing mutualisms, this represents a form of macroevolutionary hitchhiking that has been little considered. At the same time, if subdivided population structure is one of several loosely covarying features that tend to increase both speciation and extinction rates (Jablonski 2007), then it will be difficult to separate macroevolutionary effects of population structures per se from those of the mutualisms promoted by such structures—and of course this is a situation in which the two factors should be mutually reinforcing. Models testing the effects of each factor separately and together (as in Jablonski and Hunt 2006) would be valuable here.

Finally, not all endosymbioses are benign. *Wolbachia*, a microbial parasite that manipulates host reproduction to enhance its own cytoplasmic transmission, has been the subject of intense study. Evidence is accumulating that *Wolbachia* can facilitate or even drive speciation of the host (Hurst and Werren 2001; Bordenstein 2003; Telschow et al. 2005; Jaenike et al. 2006; Bordenstein and Werren 2007; but see Champion de Crespigny and Wedell 2007). Conversely, selection for limiting the impact of these and other parasites might favor strongly subdivided populations and so promote speciation (e.g., Ardlie 1998; Werren and Beukeboom 1998; van Boven and Weissing 1999; Hatcher 2000; Hatcher et al. 2000). The intensity of *Wolbachia* infection varies widely among clades (as high as ~70% of Australian and Panamanian species of fig wasps [Haine and Cook 2005], but with the global average for insects closer to 20% [Werren and Windsor 2000]), which should prompt comparative tests of the broader macroevolutionary impact of these intracellular parasites. However, a much broader array of cytoplasmic symbionts awaits analysis before the macroevolutionary role of this mode of clade interaction can be assessed (e.g., Weeks and Breeuwer 2003). Even for *Wolbachia*, the lineage infecting filarial nematodes is apparently required for normal host development and fertility (to the extent that anti-*Wolbachia* chemotherapy shows promise against the nematode infections causing such diseases as elephantiasis and African river blindness), is transmitted only vertically, and has a smaller and more static genome than the arthropod lineages (Foster et al. 2005). Comparative analyses of the causes and macroevolutionary consequences of these different pathways have barely begun.

COMENSALISM AND AMENSALISM: ECOSYSTEM ENGINEERS

Clades allowed to diversify at a constant per-taxon rate will grow exponentially, but we do not know the extent and evolutionary impact of positive feedbacks whose dynamics outpace the intrinsic exponential. The evaluation of such dynamics is complicated by at least two considerations. First, many diversity trajectories

in the fossil record that suggest positive feedbacks (e.g., following mass extinctions; Kirchner and Weil 2000; Erwin 2001) appear to be indistinguishable from sampling artifacts (e.g., Foote 2003; Lu et al. 2006; but see Wagner et al. 2006, who argue that the change in abundance structure between Paleozoic and post-Paleozoic marine communities, with an increase in rare species, suggests positive diversity feedbacks). Second, positive feedbacks might operate outside situations of unfettered diversification, so that a clade can fall short of pure exponential growth but above that produced in the absence of positive feedbacks, rendering empirical tests difficult. One approach is to evaluate differences in positive diversity feedbacks among geographic regions. However, the tendency for diversity to be highest in topographically and environmentally complex areas adds alternative controlling factors that can be difficult to exclude (see also Sax et al. 2007 on the positive relation between invasive species and standing diversity, already mentioned). For example, Emerson and Kolm (2005) found the number of endemic plant species on 5 of 7 Canary Islands to be positively related to the number of nonendemics, but both data and interpretations have been debated (Cadena et al. 2005; Kiflawi et al. 2007; Whittaker et al. 2007, and replies; for Hawaiian endemics, arthropod diversity is as significantly correlated to island altitude, and plant diversity more significantly correlated to altitude and proximity to other islands than to nonendemic diversity, according to Emerson and Kolm 2005).

Despite these analytical issues, species must often create opportunities for speciation or damp extinction probabilities of other species (Jones et al. 1997; Farrell 1998; Odling-Smee et al. 2003; Crespi 2004; Strauss et al. 2006; Valiente-Banuet et al. 2006). A predictive theory for when these effects are significant for macroevolutionary dynamics is sorely needed. This is a far cry from Darwin's wedge metaphor, which emphasized ecological replacements via biotic interactions but no positive feedbacks, and related models with static or abiotically set niche landscapes or carrying capacities (e.g., Valentine 1980; Walker and Valentine 1984; DiMichele et al. 2001). However, such models should be valuable as providing a null expectation—evolutionary diversification without significant positive feedbacks—and so deserve renewed attention.

One mechanism for positive evolutionary feedback is physical ecosystem engineering, wherein organisms modify, create, or maintain habitats (e.g., Jones et al. 1997; Hastings et al. 2007; Jones and Gutiérrez 2007; see also Odling-Smee et al. 2003 and Laland and Sterelny 2006, who define niche construction as any situation in which organisms “through their metabolism, their activities, and their choices, modify their own and/or others’ niches,” a sweeping concept that risks blurring useful distinctions, see Dawkins 2004; Okasha 2005). This effect can be seen in macroevolutionary terms in the impact of coral reefs on the diversification of molluscs, fish, and other groups (e.g., Alfaro et al.

2007; Johnson et al. 2007; see also Reaka-Kudla 1997). This large-scale interaction is even more intriguing in light of the apparent extinction-proneness of reef-building corals, creating the potential for extensive coextinctions among reef-inhabiting clades. Each reinitiation of topographically complex reef ecosystems should provide a natural experiment in the macroevolutionary impact of ecosystem engineering.

Ecosystem engineers can of course adversely affect co-occurring taxa, from shading by forest trees to flooding by beaver dams to paving by parking lots (e.g., Jones et al. 1997; van Wassenbeeck et al. 2007). Thus the abundance and/or diversification of two clades might be antagonistically coupled over long timescales without any direct competition or predation, but such dynamics have rarely been investigated. One promising and long-discussed system involves bioturbation. Marine and freshwater burrowers significantly alter mass properties and chemistry of the sediment, strongly affecting coexisting species, for example by excluding taxa requiring firm substrata or unable to clear turbidity from feeding or respiratory structures (e.g., Levinton 1995; Widdicombe et al. 2000; Austen et al. 2002; Mermillod-Blondin and Rosenberg 2006). The fabric of marine rocks shows that bioturbation intensified significantly near the start of the Cambrian, as the size, abundance, and (perhaps) activity levels of burrowers increased (e.g., Thayer 1983; Droser and Bottjer 1993). This biotic disturbance evidently disrupted sediment-stabilizing microbial mats, and sessile groups that had lived on or within mat-coated sediments in the latest Precambrian and Early Cambrian became extinct, or evolved adaptations for attachment to hard substrata (Sprinkle and Guensberg 1995; Seilacher 1999; Bottjer et al. 2000; Dornbos and Bottjer 2000; Dornbos 2006; Marengo and Bottjer 2007) (Fig. 5). Extreme drops in bioturbation intensity after several mass extinctions (as reflected in resurgences of microbial mats) show intriguing potential for comparative analyses (e.g., Sheehan and Harris 2004; Baud et al. 2007; Kershaw et al. 2007). These anachronistic occurrences—at the scale of entire lithologies!—are not quite a natural replication of the Cambrian “Substrate Revolution” because many of the groups that depended on stable seafloors were long gone. However, as with reefs, the reassembly of bioturbation communities and the positive and negative macroevolutionary consequences for other clades should be examined in a comparative phylogenetic context (and see Aberhan et al.’s 2006 finding of significant negative effects of Jurassic burrowers on sessile marine surface-dwellers).

As with escalation systems, a few data suggest that evolutionary responses to bioturbators were often accomplished by taxon sorting rather than by microevolutionary adjustments. I have seen no examples of intraspecific evolution of hard-substratum adaptations in Cambrian echinoderms, but systematic and spatially explicit analyses of biotic responses to increases in bioturbation intensity are sorely needed (for interesting targets see Sprinkle and

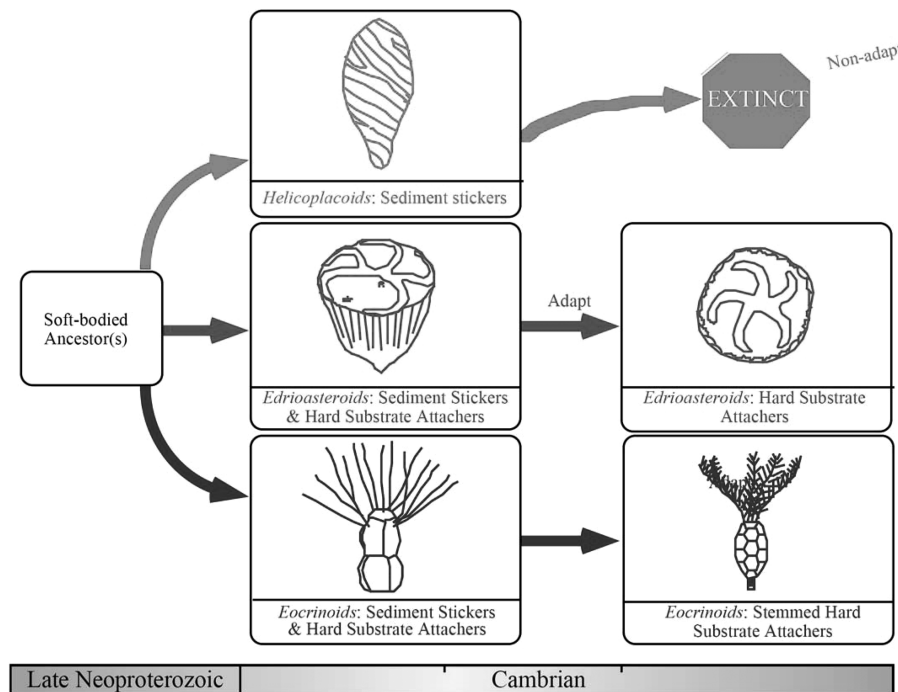


Figure 5. Macroevolutionary effects of ecosystem engineering by bioturbators. Prior to the increase in bioturbation intensity in the early Cambrian, these sessile, suspension-feeding echinoderm groups could persist partly embedded within the sediment (“sediment-stickers”). Helicoplacoids evidently had no other options and can become extinct; edrioasteroid lineages were evidently sorted according to substratum use, and eocrinoids lost their sediment-sticking clades and evolved attachment stems. Temporal pattern highly diagrammatic and shows general trends rather than direct temporal or evolutionary relationships. Schematic helicoplacoid is 3-cm long; for edrioasteroids, *Camptostroma* (left) is 5 cm in height, schematic edrioasteroid (right) is 5 cm in width; for eocrinoids, *Lichenoides* (left) is ca. 2.5 cm in height. *Tattonkacystis* (right) is ca. 5 cm in height. After Bottjer et al. (2000), used by permission.

Bell 1978; Sprinkle and Guensburg 1995). The complex evolutionary paths followed by many taxa once dependent on hard substrata within predominantly sedimentary habitats (e.g., Seilacher 2005) strongly suggests that similar linear expectations from short-term observations will rarely be met, even when the broad outlines of the clade interaction are clear. As in many other situations, the most important bioturbators (e.g., annelids, holothurians, see Thayer 1983) have poor preservation potential relative to the taxa they were undermining (again largely invalidating the global taxonomic analyses of Madin et al. 2006). Quantitative analysis of the disturbance of sedimentary fabrics offers an independent measure of the engineering effects of the biota as a whole, the difficulty being to tie such measures to phylogenetic events, and here too spatially explicit data may be useful.

Conclusion

Assessing the macroevolutionary role of biotic interactions is one of the major challenges to our understanding of large-scale biodiversity patterns. Hypotheses are difficult to test definitively, and extrapolation from short-term interactions is clearly unreliable. Several elements fall naturally into a research agenda for this area.

(1) Theory is needed that accounts for the disparate macroevolutionary outcomes of biotic interactions of organisms shown in Table 1. The effects of interactions sometimes change sign when moving across levels, and we need to understand how this mismatch works. Just as meta-analysis has begun to point to a general theory on the role of resources and consumers in regulating producer diversity in ecological communities (Hillebrand et al. 2007), the accumulation of case studies here, motivated by developing theory, could make real progress. The potential for indirect macroevolutionary effects, as when interactions affect factors contributing to speciation or extinction rates such as body size or species-level properties such as genetic population structures or range dimensions, has barely been explored (but see Thompson 2005).

(2) The notion that either the abiotic or the biotic environment shapes macroevolution is almost certainly an unproductive dichotomy. Models are needed for how biotic interactions play off against abiotic factors (and against properties intrinsic to clades at the genomic, organismic, and species level) to shape large-scale evolutionary patterns. We need to develop general rules behind variations in the relative impact of biotic factors. For example, biotic interactions seem more likely to dominate rate-determining

factors when the geographic ranges of one clade's species are consistently nested within those of the other interacting clade.

(3) Interdisciplinary efforts that focus on systems accessible to both neontologists and paleontologists are needed to promote more robust cross-level and cross-scale analysis. Paleobiologists are limited in the kinds of ecological systems that they can analyze, but a major step would be to develop evolutionary-ecological theory, models and experiments targeting a modern system well represented in the Cenozoic fossil record (e.g., soft-bottom molluscs, skeletonized marine microplankton, genus-level angiosperm pollen). Ecologists often increase tractability by restricting study to phylogenetic or functional subsets of communities and food webs, and this highly productive strategy should be adjusted to frame hypotheses for the dynamics of the most preservable clades in target ecosystems. We need models for the macroevolutionary and macroecological effects of biotic interactions in oceanic plankton communities that can be tested using just the temporal and spatial dynamics of foraminifera, diatoms, radiolarians, and coccolithophorans; or for reef ecosystem dynamics using just corals, calcareous sponges, foraminifera, and shelled molluscs.

A few paleontological systems, including plants and phytophagous insects and competitors on marine subtidal hard-substrata, can provide high-resolution snapshots of biotic interactions, but paleo and neo analyses there have been nearly independent. Challenges remain, as with the high variation in preservability among the interactors and the need to integrate those local snapshots into long term but discontinuous sequences, but the potential for deeper insights is strong. Given a set of interactions today or in the past, what are the expected macroevolutionary consequences that can be measured (to paraphrase Raup's [1988] memorable wording), and given the features of clades today, what unique dynamics must their deep-time histories (taxonomic, morphologic, spatial) exhibit to corroborate an hypothesized first-order role for a set of interactions?

More generally, neontological models and data are needed that explicitly provide expectations when time resolution is coarsened to the 10^3 - to 10^6 -year scale (depending on the age of the time window), and when taxonomy is coarsened to the genus level, as is standard practice for such promising paleontological systems as pollen and phytophagous insects. Clearly, large paleontological datasets that are robust at the species level have special value as bridges between micro- and macroevolutionary scales, and should be developed wherever feasible (see for example Jablonski and Roy 2003; Coope 2004; Graham 2005; Hunt 2007a; Webster 2007). Nonetheless, a better understanding of when genera provide a robust (if damped) proxy for standing species richness and dynamics should be a high priority; a start can be found in the conservation biology literature, where biodiversity proxies at higher taxonomic levels are frequently evaluated. The degree of congru-

ence of genetically versus morphologically defined genera varies significantly among clades but is high in some key components of the fossil record (Jablonski et al. 2006b, and in review). On the other hand, spatial and temporal variations in species/genus ratios within clades impose interesting challenges (e.g., Flessa and Jablonski 1985; Roy et al. 1996; Krug et al. 2007).

(4) Paleontologists have rarely made full use of the spatial and temporal fabric of the fossil record in evaluating hypotheses of clade interaction. The timing and location of the acquisition of a predatory, competitive, or mutualistic capability, and how this matches the supposed biotic impact can be analyzed even when (as in most cases) the interactors have differing preservation potentials. It is shocking that we have not seen a new generation of models for macroevolutionary dynamics of interacting clades that, for example, dissect diversity more finely in phylogenetic terms, take positive effects more fully into account, or are spatially explicit. Concerns about the quality of the global fossil record are well founded, but much progress has been made in paleobiology simply by recognizing that the fossil record can neither be taken precisely at face value nor dismissed as noise overwhelming signal, and regional or clade-based analyses have already been shown to be highly productive.

(5) In immediate, pragmatic terms, we need to foster more sustained interactions among fields. A postdoctoral program that puts evolutionary ecology PhDs into paleontology laboratories and paleontology PhDs into evolutionary ecology laboratories would be one way to intensify the exchange, and almost certainly would generate novel approaches to these issues. A repeat of the influential 1998 Penrose conference "Linking Spatial and Temporal Scales in Paleoeology and Ecology," with the express aim of promoting collaborations and research consortia would be another overdue step. Stronger and more continuous intellectual exchange between these two vibrant fields would be the most productive course of all.

ACKNOWLEDGMENTS

I thank G. Hunt, D. H. Erwin, S. M. Kidwell, D. S. Schemske, J. N. Thompson, and J. W. Valentine for valuable reviews, and K. Roy and S. M. Stanley for discussion and preprints. My research, and this synthesis, was supported by NSF, the John Simon Guggenheim Memorial Foundation, and NASA.

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Associate Editor: M. Rausher