Reflections on Community Ecology and the Community of Ecology: The View From a 1998 Penrose Conference on *"Linking Spatial and Temporal Scales in Paleoecology and Ecology"*

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My uncle was Albert Einstein's lawyer. Well, O.K., truth be told, he was really just a friend of Einstein's and one time when Einstein's daughter needed a divorce lawyer he called up Uncle Edgar to help him out. After the divorce, because my uncle wouldn't accept any payment for services rendered, Einstein gave him a signed photograph, which today, 50 years later, sits in my parents house.

I've been thinking about that photo a lot lately, reflecting on Einstein's lifelong interest in the relationship between time and space. Paleoecologists and ecologists have an obsessive interest in that relationship as well, albeit from a very different perspective than that of theoretical physics. During May 14–18 of this year Dale Springer, Pete Holterhoff, Jim Brown, and I convened a Penrose Conference to explore this subject with like-minded colleagues in paleoecology and ecology. The task laid out before the conferees was both to plot out new and collaborative research directions in studying temporal and spatial scaling in ecology and paleoecology, and to develop bridges across the cultural gulf separating paleoecology and ecology.

My own interest in these subjects stems from my research work on the evolutionary ecology and paleoecology of Lake Tanganyika, Africa. This large (34,000km^2, 1470m deep) and ancient rift valley lake (~10Ma) has a remarkably complex biota. At least 1500 species of protists, invertebrates, and fish have been described from Lake Tanganyika, over 600 of which are endemic to that lake. Endemicity is high even at the generic level in the lake, with a high degree of morphological and molecular genetic disparity evident in the fauna relative to congeners outside the lake. Studies of cichlid fish communities in the lake by some of my ichthyology colleagues over the past twenty years have suggested that rocky substrate, littoral communities are highly integrated, involving extreme feeding specializations and interspecific mutualisms. This view of African cichlid community dynamics actually is pervasive in the research community studying not just the cichlid fishes of Lake Tanganyika, but other lakes bearing diverse cichlid faunas as well.

However, when my students and I began to look at longer time series of paleoecological data on the benthic ostracodes of Lake Tanganyika, we saw a rather different pattern emerging. Because of the combination of high sedimentation rates (>1mm/yr) and minimal bioturbation in the lake sediments we were coring, we can obtain records that can be resolved down to about one sample per decade for benthic organisms, over time periods of thousands of years. Unlike the fish data, our data set suggested a combination of considerable turnover in the species composition of ostracode communities, accompanied by remarkable stability in total diversity over the last ~1000 years. I interpret these fossil ostracode assemblages to represent the paleoecological manifestation of a system of highly dynamic metapopulations, continuously colonizing the core sites and subsequently going locally extinct. High yet relatively constant diversity levels may be achieved by the continuous resampling (through near random recruitment) of the regional ostracode species pool (modern species distributions of ostracodes in Lake Tanganyika are extremely patchy).

Based on their long term ecological observations of cichlid fishes, my ichthyology colleagues are developing a highly "Clementsian" view of community structure in Lake Tanganyika. They see the cichlid communities as highly organized and deterministic entities, with organisms playing well-established roles within a community. On the other hand, my ostracode paleoecology data from the same lake lead me towards a more individualistic viewpoint, with species presence, absence, or abundance highly variable. My interpretation of this pattern is that ostracodes may be dependent on erratic patterns of recruitment than on obligate ecological interactions. Are these differences in interpretation the result of real biological differences in community structure and dynamics for the two groups of organisms (rocky littoral fish vs. muddy-bottom crustaceans), or are they the result of perceptual differences from coming at the problem from very different temporal and spatial scales of observation, or do they represent real differences in process or dynamics moving between time scales?

Community structure and dynamics form but two of the many issues in ecology and paleoecology whose resolution may depend on either our scale of perception or the possibility that processes differ in importance across scale "boundaries". Controversies surrounding temporal and spatial changes in guild structure, body size change, and organismal physiology are equally wrapped up in concerns about observational scale. All of these issues surfaced at the recent Penrose conference. Our conference was held at Solomon's, Maryland, on the shores of the Chesapeake Bay, to take advantage of nearby Long-Term Ecological Research (LTER) Site and paleoecology field trip possibilities. Over the course of five days about 80 ecologists and paleoecologists discussed a diversity of issues, ranging from understanding how to connect observations over the LTER or Quaternary time scales to the remainder of the Phanerozoic, to examining how ecological processes at one hierarchical level of time, space, or clades may reverberate at another level.

Questions about scaling were examined from a number of largely independent sources during the conference. Modern ecological data, in particular synoptic data from long term ecological research sites or distributional surveys, provides us with a wealth of detail obtained from direct observation of species interactions, body size and shape variation, abiotic forcing of distributions, behavior,

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and diversity. Bruce Patterson showed how patterns of species turnover vary between clades along altitudinal gradients in the Amazon basin. Zonation patterns for birds have been used frequently as proxies for understanding regional biotic distribution. However, Patterson showed that bird (and bat) zonations, which are largely nondiscrete across elevational gradients, are quite different from the discrete zonation patterns seen in rodents. These differences are probably historical, relating perhaps to differential dispersal over time in the various groups, but without confirmatory data over longer time intervals it is difficult, if not impossible, to test this hypothesis. Similarly, Fred Grassle presented data concerning the extreme patchiness of deep sea organisms accompanying the well-known high diversity of this habitat. Small scale heterogeneity seems to be regulated by the presence of features such as logs, clumps of debris, or current scours, features whose formation or persistence could in principle be observed through repeat observation (though in the deep sea, where observational costs are a major issue, even this is problematic). But what about longer term or much larger spatial scale processes that may regulate heterogeneity over, say, the scale of ocean basins? Such processes are unlikely to be directly observed by ecologists.

This point illustrates the fundamental limitation of most neoecological data: the fact that they are inevitably of short duration, often regulated more by grant and graduate student cycles than by nature. Hence, they cannot uncover the deep historical underpinnings of species adaptations, associations, or distribution patterns. To paraphrase one ecologist participating in the Penrose Conference, after he heard a paleoecologist bemoaning problems of time averaging in fossil assemblages, "I only wish that our ecological data were more time averaged, to get away from short term vagaries and stochasticity of sampling!"

Paleoecological data, of course, provide us with long time series information, sufficient to determine the historical background of ecological associations, patterns of diversity change, body size fluctuations, or guild structure. This increased time window comes at a cost of decreased temporal resolution (though, as I noted above, this may be a good thing, for appropriately scaled questions), along with a weaker base for inferring process from pattern, as well as the obvious loss of information concerning nonfossilized components of the ecosystem. This combination of advantages and liabilities was evident from the extensive conference discussions, particularly regarding the contentious subjects of coordinated stasis and the representativeness of patterns of Quaternary ecological change for the remainder of the Phanerozoic. Linda Ivany presented the case for coordinated stasis as a pervasive pattern of ecological structure , based on her data from the Gulf Coast (U.S.) Eocene, along with Carl Brett and Gordon Baird's work on the Devonian Hamilton Group of New York. In contrast, Mark Patzkowski, Russ Graham, and Steve Jackson all argued for a more individualistic pattern of biotic compositional change, based on Ordovician and Quaternary data. Do these differences in opinion reflect real differences in the structure of diversity change between specific time intervals of Earth history, or are they the result again of under- or over-resolution of data sets to answer specific questions? The truth is that we just don't know yet, and in several panel discussions and informal workshops during the meeting there was a clear call for paleoecologists to attack this problem via broad comparisons of multiple data sets.

Conference participants (and in particular, the non-paleoecologist participants) got a chance to evaluate the nature of paleoecological data sets and both the constraints and advantages imparted by the long term time-averaging of the marine fossil record during the second conference field trip to the well known Miocene Calvert Cliffs. Susan Kidwell and Patricia Kelley led a stimulating tour of the outcrops which have played a key role in many important debates about inference of ecological interactions in the fossil record. The field trip leaders discussed the interpretations by Kidwell concerning both the completeness and temporal organization of the fossil shell beds and the evidence for work by Kelley and her coworker Thor Hansen concerning both predator prey interactions and cyclic escalation in those interactions.

Another recurrent theme at the conference was a call to understand the interactions between differently scaled processes. Arnie Miller showed that when you "dissect" the pattern of global diversity change in the Ordovician, a much "spikier" pattern of change emerges at the regional scale, probably related to the differing tectonic histories of individual regions. Is a global pattern of smoothed ecological change then more than the sum of its erratic regional parts? Do events in the early history of clade diversification set the pace for subsequent change of diversity or ecomorphic guild structure? Presentations by both Dave Jablonski and Bill DiMichele seem to suggest that such across-scale interactions may be important phenomena, but, as numerous participants noted, ultimately it will take concerted collaboration between specialists at differing scales to understand the dynamics of these linkages. Joan Roughgarden examined the linkages between the local and oceanic transport scales in determining patterns of barnacle recruitment in the Pacific coastal intertidal. Competition and predation experiments of the 1970s gave ecological theorists hope of gaining general understanding of these classic interactions based strictly on local phenomena. Their nonreproducibility in different biogeographic settings suggested that other, larger scale phenomena, may play a role in determining the reproducibility of this interaction. Roughgarden has shown that the large scale recruitment process, regulated by ocean currents, must be integrated with the small or local scale population patch observations to come up with a broadly predictive model. No one scale holds the entire story!

The first conference field trip also illustrated the importance of examining the linkages between scales in ecology. The dominant theme of long term ecological change in the Virginia Coastal Reserve is relative sea level change. An outstanding first day field trip to this area was organized by Bruce Hayden and John Porter, and lead by Porter, Ray Dueser, Mike Fenster, Aaron Mills, Linda Blum, and Bob Christian. In some areas of the Delmarva Peninsula, sea level rise and its consequent conversion of freshwater to brackish water marshlands is modulated by the echoes of an Eocene bolide impact, with its differential effects on local subsidence. Intermediate-scale (post-Pleistocene eustacy) and short term (anthropogenic) processes interact with this background to produce patterns of ecological change that are utterly unpredictable based on knowledge of any single scale.

Another approach to understanding the history of diversity, ecological structure, and interaction can come from phylogenetic inference. This can be very informative in the case of, for example, host-parasite relationships, or other species groups that are linked by strong interactions. It provides a means of testing hypotheses of relationships between ecological and evolutionary patterns, although the temporal and spatial resolution that can be mapped onto a given tree will depend on the quality of the associated data rather than the tree itself. Although conference participants noted the importance of a phylogenetic approach to macroecology and their desire to establish connections with these colleagues, this perspective was clearly under-represented at the meeting. In panel discussions this was recognized as a very promising direction for new research on scaling phenomena.

Our original impetus for organizing this conference was to specifically address the theme of temporal and spatial scaling common to paleoecologists and ecologists. However, by the second day of the meeting it was evident that a broad agenda was possible, to create "cultural" bridges across the neo/paleo ecology divide, demonstrated by our individual jargon and the broad concepts (or biases) behind them. Ecologists are informed by landscape fragmentation, stable attractors, and resilience, while Quaternary paleoecologists worry about Dansgard-Oeschger Cycles, Heinrich Events, and Stage 5e, and pre-Quaternary paleoecologists talk about 3rd order sequences, bolides, and accreted terranes. On one level, these terms reflect our differently scaled concerns about the dynamics and forcing processes regulating the Earth's ecosystems. But the fact that most of us probably can't correctly define all of these terms (except maybe for graduate students who have just been studying for preliminary exams) also indicates that we have been operating in our own ecosystems for too long. Much of the meeting therefore was devoted to considering how to bridge this cultural gulf. Jim Reichman of the National Center for Ecological Analysis and Synthesis (NCEAS) gave a stimulating talk the first evening of the meeting explaining how NCEAS is eager to support working study groups and sabbatical visits (among other means) specifically to address many of the broad points of contact that were being raised between the various research communities at the meeting. No fewer than 17 topics for cross disciplinary working groups were proposed during one of the panel discussions, and even if only a handful of these projects move forward, the synthesis we (the organizers) had hoped to promote will have moved dramatically forward. Progress towards such syntheses will take time but the corridors are certainly in place for intellectual migrations between the diverse disciplinary patches of ecology and paleoecology to occur.

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