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SPOTLIGHT

CRITICAL ISSUES OF SCALE IN PALEOECOLOGY

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In mid-September 2007, 32 paleontologists gathered at the Smithsonian Institution to spend four days discussing research frontiers in paleoecology, particularly at the interface with neoecology. They represented expertise throughout the Phanerozoic and in all major groups of fossilizable organisms. This meeting was timely, given the increasing evidence of the impact of climate change on ecosystems in our modern world. The vast repository of paleoecological data on past environmental change and concomitant ecological responses, observed at many different spatial, temporal, and taxonomic scales, is of potentially great value for understanding and predicting how modern ecosystems will respond to climate change. Of particular interest to the participants of this meeting were questions of how ecological data collected at different scales could be reconciled so that our knowledge of ecological change in the past can better inform our understanding of the present and our predictions of how ecosystems will change in the future. Certainly, this is one of the most exciting research frontiers in paleoecology.

Data collected for different ecological studies (both paleoecological and neoecological) encompass a wide range of spatial, temporal, and taxonomic scales. Understanding the scales inherent in an ecological research question is critical to designing a sampling protocol that will yield data capable of resolving that question, yet these scales are often not adequately evaluated or presented in published paleoecological reports. Furthermore, for any body of paleoecological research to be rescued from isolation and integrated with other studies, the various scales encompassed by the research questions and data must be understood and reported.

The greatest barrier to communicating and collaborating with neoecologists is not that data collected from extant ecosystems are necessarily different or more complete than paleoecological data but, rather, that these two data sets commonly represent or are collected at different scales. If such differences of scale can be understood and quantified, then they can be reconciled and even exploited. This will allow neoecological studies to inform the interpretation of patterns and processes in the fossil record and will permit the use of paleoecological studies to test how ecological and environmental processes have structured the biosphere over extended time intervals (National Research Council, 2005). To facilitate better communication and sharing of data among paleoecologists and neoecologists, we offer the following guide to questions of scale that we recommend be explicitly addressed to the fullest extent possible in any paleoecological research report. We consider the following a checklist—one that we hope will be useful, particularly to those embarking on new research. For those seeking an important research problem to tackle, we end with a list of significant, yet still unresolved, scale-related questions.

GENERAL ISSUES OF SCALE

Issues of scale are inherent in all paleoecological studies and must be considered from the outset of any research program. Experience shows that awareness of scale and its effects—on everything from the questions posed to the way data are sampled and analyzed—evolves in the course of a paleoecological investigation. Beginning with some basic considerations will facilitate the incorporation of scale into our scientific endeavors.

What Is the Objective of the Study, and What Questions Are Being Asked?

How are the potential answers to paleoecological questions dependent on spatial and temporal scales? What kinds of samples are needed to provide the spatial and temporal scale appropriate to these questions? What constraints on sampling are imposed by the availability and geographic extent of outcrop or by the stratigraphy and taphonomy of the fossiliferous sediments (e.g., Patzkowsky and Holland, 2003)? Will these constraints generate a mismatch between the scale of sampling and the scale of the questions being asked?

What Parameters of Scale Are Defined in the Study?

What are the functional ecological units of the study, that is, at what spatial and temporal scales are individual fossils considered members of the same community or paleocommunity (e.g., Bambach and Bennington, 1996; Fortelius et al., 2002; Kovar-Eder et al., 2008)? At what spatial and temporal scales are fossils inferred to have occupied the same habitat (e.g., Barrett and Willis, 2001; Strömberg, 2006)? Are there spatial or

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Participants in the Smithsonian Evolution of Terrestrial Ecosystems Workshop, Paleontological Powers of Ten: Issues of Scale in Paleoecology, held at the National Museum of Natural History, Washington, D.C., United States, in September 2007. First row kneeling, left to right: Seth Finnegan, Ellen Currano, Gene Hunt, Philip Novack-Gottshall, Caroline Strömberg, Michal Kowalewski. Second row left: Bonnie Jacobs, Cindy Looy, Anna Behrensmeyer, William DiMichele, Robyn Burnham. Second row right: Hannah Bonner, Catherine Badgley, Kate Lyons, Sara Williams, Susan Kidwell, Stephen Jackson, René Bobe, Peter Roopnarine, Ted Daeschler, Stefan Little. Last row left: Peter Wilf, Jan van Dam, Bret Bennington, David Jablonski, Hans-Dieter Sues, Scott Wing, Conrad Labandeira, Richard Bambach, Steve Holland, Peter Wagner, Paul Koch, Jussi Eronen, Paul Barrett. Not in picture: Douglas Erwin, Richard Potts (photo by Chip Clark).

temporal scales at which stasis or equilibrium of taxonomic composition, relative abundance, and so forth, is inferred or defined as a baseline for evaluating changes at different scales (e.g., Bennington and Bambach, 1996; Holland and Patzkowsky, 2004; DiMichele et al., 2004)?

SAMPLING DESIGN—HOW WERE THE DATA COLLECTED?

Every research report should include a description of the sampling protocol that explains how samples were collected and processed in detail sufficient to allow another investigator to exactly replicate the sampling. The report should also explain how the deployment of samples addresses the issues of scale relevant to the research questions posed (e.g., see papers cited in DiMichele and Wing, 1988; also Miller, 1990; Wing et al., 1993; Hayek and Buzas, 1997; Jones and Rowe, 1999; Gastaldo and DiMichele, 2000; Strömberg, 2006). Important elements of sampling design and description include the following five topics:

1. *Sedimentological and Taphonomic Context.*—What was the depositional context and preservational mode of the samples, including descriptions of the sedimentary matrix, degree of lithification, diagenetic alteration, biostratinomy, and taphonomic condition of the fossils (e.g., Brett and Baird, 1986; Behrensmeyer and Hook, 1992)? What was the sequence-stratigraphic context of the samples, that is, their position within systems tracts or relative to such important horizons as flooding surfaces and sequence boundaries (e.g., Holland, 2000)? What were the approximate dimensions (area, water depth) of the depositional basin?

2. *Nature of the Samples.*—How were fossils obtained and enumerated (e.g., Badgley, 1986)? Were bulk samples or bedding planes counted? What was the approximate volume or area of each sample? What was the screen size used when sieving samples? Was the density of fossils consistent from sample to sample, or did some samples require a larger volume or area to produce comparable numbers of fossils? Were all specimens counted or were subsamples counted? If the latter, how was the statistical robustness of sample estimates (diversity, frequencies, ratios) ensured (e.g., Raup, 1975; Jamniczky et al., 2003)? How were fossils extracted from the matrix? Did the methods used to extract fossils introduce any biases caused by size, shape, density, differential mineralogy, or preservation (e.g., Strömberg, 2007)? How were numbers of individual organisms estimated from bivalved and other multi-element fossils (e.g., Wolff, 1975)? Were taxa represented by different numbers of body parts weighted differently in the analysis?

3. *Spatial Distribution of Samples.*—How were sampling sites arrayed in space relative to geography and the distribution of sedimentological units and facies (e.g., Wing et al., 1993, 1995; Strömberg et al., 2007)? What was the lateral and vertical spacing between sampling sites, and how consistent is it? Did the sampling sites constitute one or more transects relative to the regional setting? Were multiple samples collected at sites? Were samples grouped into different levels of a spatial hierarchy (e.g., groups of replicates at a point along an outcrop, multiple points sampled along an outcrop, multiple outcrops sampled within a region; see, e.g., Wing et al., 1993; Bennington, 2003; Burnham et al., 2005)?

4. *Temporal Distribution of Samples.*—How were isochronous samples identified? What stratigraphic markers were used to define temporal sampling intervals? How temporally constrained were sample sites and samples? What was the total stratigraphic and temporal range encompassed by samples in the study? Were there gaps in the temporal distribution of samples (e.g., Sheehan et al., 2000; Wilson, 2005), and how did the gaps affect the sampling design?

5. *Sample Replicates.*—How many replicates of each sample were collected, and what was the spatial and temporal distribution of replicates (e.g., Bennington and Bambach, 1996)?

RELATING PALEOECOLOGICAL SAMPLES TO NEOECOLOGICAL SPATIAL AND TEMPORAL SCALES

Perhaps the most challenging questions to answer in any study are the ones that relate the spatial and temporal scales of samples to the inferred spatial distribution and temporal range of the ancient ecosystem(s) (e.g., Burnham, 1993). Fortunately, there is a large body of literature in paleontology, much of it based on actualistic studies, that addresses the formation of fossil assemblages and provides guidance for inferring the degree of spatial mixing and time averaging of the living community that occurred to produce the fossil assemblage (e.g., papers cited in Kidwell and Behrensmeyer, 1993; Kidwell and Flessa, 1995; papers cited in Behrensmeyer et al., 2000; Kidwell, 2001, 2002; Strömberg, 2004; National Research Council, 2005). For any collection of samples, one should attempt to address the following questions:

1. What is the degree of taphonomic time averaging, that is, how finely could time be resolved given the nature of the fossil assemblages in question? What is the degree of analytical time averaging, that is, how finely is time resolved, given the chosen sampling design? Together, these two questions constrain an estimate of how much ecological time has been condensed into the paleontological samples, which is the most important issue of temporal scale in paleoecology.
2. The most important aspect of spatial scale is the relationship between the individual samples of rocks and fossils (e.g., bulk samples) and the population of interest to the researcher doing the sampling. How much ecological assemblage space is captured in an individual sample, or how much do we believe to be captured by reference to actualistic studies (e.g., Burnham et al., 1992; Strömberg, 2004)? How much space does the suite of samples deployed in the study capture?

BIOLOGICAL ISSUES OF SCALE

Matters of scale relating to the biology of the organisms being sampled arise in both paleoecology and neoecology. One important aspect of any study is the taxonomic resolution of the analysis. Were the organisms analyzed at a particular taxonomic level or as some kind of functional or ecological guild (e.g., Erwin et al., 1987; Damuth et al., 1992; Wing et al., 1992; Strömberg, 2004; Novack-Gottshall, 2007)? Another aspect of biological scale is the size range and skeletal complexity of the organisms being captured in the samples. At what size were smaller or, in some cases, larger organisms excluded from the analysis because of the limitations of sample acquisition and processing (e.g., Bush et al., 2007)? Finally, which components of a community were excluded from the fossil assemblage or from the samples by taphonomic factors (e.g., understory plants are often undersampled in paleobotanical and pollen assemblages; see Scheihing, 1980; Jackson, 1994)? These aspects of biological scale are important for establishing the comparability of data between paleoecological and neoecological studies.

QUESTIONS FOR NEW RESEARCH

Finally, we note a range of interesting questions related to sampling that should be addressed by new research and meta-analyses facilitated by explicitly defined sampling:

1. How does the distribution of sampling effort at smaller spatial and temporal scales affect the conclusions reached by analyses of data at larger spatial and temporal scales (e.g., Novack-Gottshall and Miller, 2003a, 2003b)? What is the impact of sampling scale on analyses of paleoecological patterns and trends? Are patterns seen in data collected at one scale robust when tested against data collected at smaller or larger scales?
2. How does sampling at different spatial and temporal scales affect reconstructions of paleoecosystem composition and dynamics?
3. How does taxonomic resolution affect the analysis of paleoecological patterns?
4. To what degree are paleoecological samples from a hierarchy of temporal scales equivalent to samples from a hierarchy of spatial scales? Can expanded temporal sampling serve as a proxy for expanded spatial sampling or vice versa?
5. How do paleoecological samples compare to neoecological samples in the temporal and spatial scales represented? How do measures of community composition, structure, diversity, and so on, aggregate through time averaging of communities? Can averaging over multiple samples convert a series of neoecological samples into the equivalent of a paleoecological sample? This question has been addressed by various studies involving live-dead comparisons among multiple samples of modern marine benthos (e.g., Kidwell, 2001, 2002, 2007; Lockwood and Chastant, 2006; Olszewski and Kidwell, 2007) and pollen assemblages (e.g., Birks and Gordon 1985; Sugita, 1994), but additional analyses are needed from different depositional settings and representing different groups of organisms.
6. How could neoecological or paleoecological sampling methods be adjusted to increase their reciprocal comparability? What degree of spatial, temporal, or taxonomic smoothing is required to render modern ecological samples comparable to fossil samples? What do we gain and what do we lose by such smoothing?

Overall, these questions address the comparability and compatibility of studies conducted at different spatial and temporal scales. Additional research and insight into any of the above questions would constitute a valuable contribution to the study of both modern and ancient ecosystems.

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