The multiple scales of biodiversity

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Introduction

The claim that measures of global biodiversity dynamics are meaningless is based upon several methodological problems, including underrepresentation of tropical regions in ''global'' Phanerozoic data sets, inaccuracies in taxonomic data, non-equivalence of higher taxa among groups of organisms, and uneven sampling intensity across groups, environments, and time intervals. Some of these problems are inherent in the fossil record, whereas others lie in documentation and interpretation of the subject. But the subject of global biodiversity is perfectly legitimate, even if problems persist in evaluating its full history. Moreover, recognition of the methodological problems has resulted in notable improvements in the Phanerozoic diversity database (e.g., Adrain and Westrop 2000; Alroy et al. 2001).

Here I offer three points: (1) The study of biodiversity is meaningful at many spatial and temporal scales, including the global scale. (2) Two major preservational biases limit the estimation of global biodiversity over the Phanerozoic, although estimates are still potentially meaningful. (3) Extrapolation of patterns and processes from a smaller scale to a larger one or from one clade to a more inclusive clade is inappropriate and justifies some criticisms of biodiversity studies at the largest scales. Below, I elaborate on these points from a perspective based in experience with vertebrates in terrestrial ecosystems.

Multiple Relevant Scales

Significant patterns of biological diversity and the ecological and evolutionary processes that shape them occur at multiple spatial scales, including local, regional, continental, and global, and multiple temporal scales, including those of ecological and evolutionary processes. Biological diversity itself is a multiscale concept, ranging from genetic diversity within local populations to ecosystem diversity across landscapes. Three sets of examples illustrate processes influencing biodiversity, including its protection, at different scales.

(1) Global biodiversity is meaningful partly as the sum of biodiversity measures for smaller regions, but also because it is influenced by physical and biological processes at the global scale. Phanerozoic global biodiversity for marine and terrestrial realms has been summarized by Sepkoski (1993) and Benton (1995), respectively. Processes that affect biodiversity at the global scale include plate tectonics, global climate dynamics, and eustatic sea-level changes—over timescales of decades to millions of years. These geological phenomena affect probabilities of speciation and extinction, rates of biotic turnover, the geographic distribution of biomes, dispersal among major land masses and ocean basins, and adaptive trends within lineages. The dispersed continents and ocean basins and strong latitudinal climatic gradients of the late Cenozoic appear to support greater global biodiversity than did the Pangea configuration (the supercontinent that resulted from all the continents drifting together) of the late Paleozoic and early Mesozoic. Mass extinction is a global phenomenon because the causes are global in nature, and because its recognition is based on elevated extinction rates in many regions of the world. In the conservation arena, the global reserve network proposed for modern biodiversity hotspots and conservation strategies for intervening areas require knowledge of biodiversity patterns, habitat degradation, and the magnitude and timing of extinction across the world (Pimm et al. 2001).

Only with a global perspective are the major hotspots recognized. Global warming affects biogeochemical cycles at the global scale, range boundaries of species and biomes at the regional scale, and trophic dynamics at the local scale.

(2) At the regional to continental scales, changes in species richness and ecological diversity of floras and faunas in relation to physical environmental gradients are evident. At these scales, for example, climate and topography explain much of the variation in species richness of terrestrial vertebrates and trees (e.g., Currie 1991; O'Brien 1998). Although data are gathered at the local scale, the patterns do not emerge until data are analyzed for large regions up to entire continents. At these scales, changes in climate and topography limit most species ranges, resulting in considerable spatial turnover in species richness and ecological structure. The conservation status of mobile, widespread species must be evaluated at the regional scale for understanding the magnitude of human impacts on populations and ecosystems and appropriate management responses. For example, the collapse of the North Atlantic fisheries and consequent changes in marine ecosystem dynamics over the last 50 years were unappreciated in their full magnitude until data were integrated over all major fish stocks for the entire North Atlantic Ocean (Pauly 2002). Only huge marine reserves and unprecedented reductions in fishing pressure will allow recovery of these ecosystems.

(3) At the local scale, ecological interactions among individuals and populations influence the species present and their ecological characteristics. Species may be favored or excluded by competition, predation, the intensity of disturbances, spatial heterogeneity, or seasonal variation in resource distribution, or combinations of these factors. Substantial temporal variation in species composition since the late Pleistocene and high spatial variation in species composition today characterize the granivorous rodent guild of western deserts of North America (Brown and Kurzius 1989). At the local scale, resource availability and interspecific competition determine the particular rodent species that co-occur, from a regional species pool. In the conservation arena, the viability of populations and species with extremely small ranges (e.g., the Devil's Hole pupfish, Ash Meadows, Nevada, United States, with the smallest range documented for a vertebrate species—a single pool roughly 65 m^2 in area) requires management of human and biophysical activities over areas of 10^{-1} to 10^3 km^2. The persistence of vulnerable species is enhanced when suitable habitats are linked by habitat corridors, linking local and regional scales in conservation efforts (Stein et al. 2000).

In summary, different scales are the domain of different processes and patterns.

Major Preservation Biases

The most fundamental preservation biases are the absence of major environments and soft-bodied organisms from the long-term fossil record. Long-term (>20 Myr) depositional environments originate at low elevations, on the continental shelves, and in the deep sea. High-elevation habitats and non-depositional landscapes at mid- and low elevations are represented in the fossil record only in the short term. For example, caves and lakes in mountainous regions today may contain rich fossil deposits, but these eroding landscapes will disappear over the next several million years. Over three-fourths of the earth's terrestrial habitats and the biodiversity residing in them, including the high diversity associated with mountainous areas in the Tropics, do not influence the fossil record except as downstream weathering products. In addition, most of the fossil record consists of mineralized tissues of organisms or biological materials resistant to chemical degradation, such as sporopollenin. Most organisms do not contain such tissues, so contribute only rarely to the fossil record. Lagerstätten offer a glimpse of what is absent from much of the record. These two large-scale biases distance the fossil record from the actual history of life on Earth and severely limit the estimation of global, regional, or local biodiversity before the Pleistocene. The ''pull of the Recent,'' the higher proportion of taxa documented from younger rocks (Raup 1979), results from more complete sampling and knowledge of young to

Recent taxa, resulting in range extensions (of older to Recent taxa) that would not otherwise be made. Other influences on the increased taxonomic richness approaching the present include greater exposure areas of younger strata and a wider range of younger depositional environments, including some that are transient in the fossil record. These biases do not, however, render the study of global biodiversity history meaningless. Rather, the bias against particular environments indicates that studies of Phanerozoic diversity should include a similar set of paleoenvironments over time. The bias against soft-bodied organisms is probably consistent throughout earth history and is mainly at issue in comparing modern and ancient biodiversity. The remedy is to compare the Phanerozoic diversity record with modern organisms of similar preservation potential.

Inappropriate Extrapolation

Some studies extrapolate inappropriately from smaller to larger scales. For example, various studies of spatial or temporal trends in terrestrial vertebrates focus on data from a particular region (e.g., the continental United States) but declare the results to represent an entire continent (North America). This extrapolation is inappropriate because biodiversity patterns for any major group of organisms (e.g., mammal species, tree species) vary widely within continents today (e.g., Currie 1991; Badgley and Fox 2000). In North America, diversity patterns in the Great Plains are not indicators of patterns in the highlands of Mexico or in eastern Canada. The tendency to generalize from one taxon to a larger clade, e.g., from mammals to terrestrial vertebrates, leaves the generalizations at larger scales open to criticism. Among vertebrates, geographic patterns in species richness over large-scale environmental gradients vary substantially among related higher taxa. In North America (north of Mexico), amphibians have the highest species richness per unit area in the south-eastern United States, squamates in the south-central United States, and mammals in the mountains of California (Currie 1991). Among mammals, ecologically different subsets show different geographic patterns across North America. For example, small-bodied species increase in number from high to low latitudes, whereas large-bodied species show the reverse pattern (Badgley and Fox 2000). Biodiversity studies should generalize at the spatial or taxonomic scales of their data.

In conclusion, global biodiversity is meaningful at its own scale of inquiry, and especially so in the context of diversity documented at regional and local scales as well. The most interesting work that lies ahead is the integration of patterns and processes across spatial and temporal scales.

Literature Cited

Adrain, J. M., and S. R. Westrop. 2000. An empirical assessment of taxic paleobiology. Science 289:110–112.

Alroy, J., et al. 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. Proceedings of the National Academy of Sciences USA 98:6261–6266.

Badgley, C., and D. L. Fox. 2000. Ecological biogeography of North American mammals: species density and ecological structure in relation to environmental gradients. Journal of Biogeography 27:1437–1467.

Benton, M. J. 1995. Diversification and extinction in the history of life. Science 268:52–58.

Brown, J. H., and M. Kurzius. 1989. Spatial and temporal variation in guilds of North American granivorous desert rodents. Pp. 71–90 in D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, eds. Patterns in the structure of mammalian communities. Texas Tech University Press, Lubbock.

Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. American Naturalist 137:27–49.

O'Brien, E. M. 1998. Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. Journal of Biogeography 25:379–398.

Pauly, D. 2002. Setting a baseline: world fisheries and ecosystems in 1950. American Association for the Advancement of Science Annual Meeting, 2002, Boston, Program and abstracts, p. A29.

Pimm, S. L., et al. 2001. Can we defy nature's end? Science 293:2207–2208.

Raup, D. M. 1979. Biases in the fossil record of species and genera. Bulletin of the Carnegie Museum of Natural History 13:85–91.

Sepkoski, J. J., Jr. 1993. Ten years in the library: new data confirm paleontological patterns. Paleobiology 19:43–51.

Stein, B. A., L. S. Kutner, and J. S. Adams. 2000. Precious heritage: the status of biodiversity in the United States. Oxford University Press, Oxford.