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MATTERS OF THE RECORD

Ecological patterns in time and space

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There is a fundamental debate in ecology regarding the degree to which multispecies assemblages ("communities") are coevolved and have properties beyond those of the component populations. The dialogue was framed by the plant ecologists F. O. Clements and H. A. Gleason. Clements (1916) argued that terrestrial plant communities were highly integrated superorganisms, while Gleason (1926) represented the opposing, reductionist view of communities as ephemeral, even happenstance, associations of species with similar resource requirements. Although the terms have changed, the discussion has continued, and, most recently, some ecologists have attempted to bring a hierarchical perspective to this old problem (O'Neill et al. 1986; Allen and Hoekstra 1992).

Paleoecology brings the fossil record to bear directly on ecological theories and raises questions about ecosystem organization that are uniquely answerable with data from the fossil record (Miller 1990a, 1993). Most of this work has come, and continues to come from invertebrate paleontology. However, terrestrial paleoecology has much to contribute (Behrensmeyer et al. 1992), and the patterns found in the terrestrial record are remarkably similar to those reported for marine invertebrates. This essay briefly compares the areas of convergence between marine and terrestrial paleoecology, and discusses the implications of this convergence for ecology at large.

The fossil record is generally credited only with allowing the observation of ecosystem dynamics on time spans of 10^4 yr or greater. At best this expectation sells the record short and overlooks what is perhaps its most interesting aspect, the opportunity to extend the examination of short-term ($<10^3$ yr) spatio-temporal dynamics over a wide range of time scales. This cannot be overstressed: paleoecology is not limited to providing evidence of ecosystem processes on time scales of 10^6 yr or more (e.g., Pimm 1991), but can examine the pattern and infer dynamic processes on time scales relevant to many debates in community ecology.

What perspective does paleoecological data bring? If one reads the literature of Pleistocene and Holocene terrestrial plant and vertebrate records, the conclusion is inescapable: Gleasonian "individualistic" dynamics predominate in the past as today (Graham and Grimm 1990; Overpeck et al. 1992). Species respond independently to changing climatic and edaphic conditions caused by the advance and retreat of glaciers, resulting in ephemeral communities that have no properties beyond those of the component populations. Observations from the deeper past, however, reveal that ecosystem structure and taxonomic composition commonly persist or repeatedly recur throughout intervals of hundreds of thousands to millions of years (Boucot 1983; Wing 1984; Olson 1985; Sheehan 1985; Brett et al. 1990; Brett and Baird in press; DiMichele and Phillips in press).

Comparison of Marine and Terrestrial Patterns

There are considerable parallels in the community structure and dynamics of sessile ma-

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rine benthos and terrestrial plants: lack of or limited vagility, broadcast fertilization and dispersal, and "passive" means of acquiring nutrients from the surrounding environment (in the water stream or from sunlight). Terrestrial and marine ecology also share increasing interest in scale and the possibility of levels of organization beyond those visible on short time spans (Boucot 1983; O'Neill et al. 1986; Miller 1990b).

Perhaps the clearest documentation of hierarchy in the marine realm comes from the work of Brett and colleagues on the Silurian and Devonian of New York state. In brief, these authors recognize several levels of organization. Species can be grouped into guilds, which are functional groups; any one guild tends to be filled for millions of years by the same or closely related species (Brett et al. 1990). Biofacies or recurrent assemblages are habitat-specific species groups (roughly communities) that persist for 5–6 m.y. with limited turnover or introduction. Groups of biofacies form regional faunas or ecological-evolutionary subunits (EESUs, multi-species landscapes) that also persist for long time spans (Brett and Baird in press). Biofacies and EESUs display abrupt changes during geologically brief restructuring events. At a global level, regional faunas are parts of still longer-ranging, and geographically widespread ecological-evolutionary units (sensu Boucot [1983] and Sheehan [1985]).

This terminology is unfamiliar to neoecologists. It reflects the uncertain translation of pattern in the fossil record into the classification systems of modern ecology, while attempting to provide a nomenclature that translates the spatial patterns of neoecology into the temporal patterns of paleoecology. Regardless of what the units are called, certain distinctive patterns emerge when spatially defined units are tracked through time. Biofacies persist and apparently resist invasion while remaining characteristic of particular physical settings. Species turnover during periods of assemblage persistence occurs largely on guild themes and results in one for one replacement; members of guilds tend to be closely related phylogenetically. Finally, biofacies and EESUs persist for millions of years through minor environmental perturbations, but are disrupted and destroyed by major environmental change and consequent extinctions. Following disruption, new persistent patterns of community organization emerge within time periods estimated to be much less than a million years (Brett et al. 1990). Work on Permian post-extinction landscapes (Schubert and Bottjer 1993) suggests that opportunistic taxa have an advantage during periods of ecological disruption, and are the stem lineages from which new community architectures evolve.

Patters almost identical to those described for Silurian-Devonian and early Triassic marine faunas have been documented for terrestrial floras (Cridland and Morris 1963; Wing 1984; Raymond 1993; DiMichele and Phillips in press). Floras of the Carboniferous tropics are the most thoroughly studied at a wide variety of temporal and spatial scales, and show patterns similar to those described by Brett and Baird (in press). Species can be classified into characteristic ecomorphic groups (approximately the same as guilds). Ecomorphs comprise species assemblages (communities), with characteristic quantitative dominance-diversity structure restricted to specific habitats. These species assemblages persist for up to 9 m.y., and retain their ecomorphic structure, as long as extinction levels and species turnover are relatively low, suggesting self-regulation of turnover dynamics. Species assemblages make up multi-community landscapes, which persist for 2–3 m.y. Landscapes are part of larger biomes: the Carboniferous lowland, wetland biome, for example, consists of ecological associations characteristic of swamps and mires, and fluvial-deltaic flood plains (Gastaldo 1987). Biomes are characteristic of regional to continental scale floristic provinces: the Euramerican–Cathaysian tropical province contains both wetland and mesic to xeric biomes (Cridland and Morris 1963; DiMichele and Aronson 1992).

Minor changes in successive landscapes are generally abrupt and are reflected largely in changed proportions of species assemblages (communities), possibly a consequence of changes in gradient lengths or in the average patch size occupied by any one species assemblage. Species assemblages are resistent to change in their taxonomic and ecomorphic composition and in dominance–diversity structure, and consequently may persist longer than any particular landscape configuration they comprise. Major landscape-level changes result from extreme climatic changes that apparently cause significant elevation of species extinction levels, perhaps exceeding 50% (Pfefferkorn and Thomson 1982; Phillips and Peppers 1984). Such high levels of extinction are followed initially by loss of recognizable species assemblages and poordefined landscape structure. Ultimately a new spectrum of species assemblages appears. The loss of structure at the level of species assemblage may be seen as a breakdown in the fabric of species interactions and suggests extinction thresholds that when crossed eliminate the system's ability to regulate patterns of ecomorphic species turnover. Following periods of major extinction, opportunistic species radiate rapidly and become the basis of new species assemblages (community types) and landscapes (Pfefferkorn and Thomson 1982; DiMichele et al. 1987; DiMichele and Phillips in press). Biomes, which contain the lower order dynamics, replace each other in the tropics largely as units, with little intermixing of characteristic species and probably as a consequence of progressive climatic changes (DiMichele and Aronson 1992).

The time dimension permits ecologists to study the dynamics of units that are largely spatially defined (e.g., population, community, biome). With space–time continuity, it can be seen that each spatial unit may have certain characteristic long-term behaviors. Descriptors common to both the marine and terrestrial realms include multiple levels of organization with partially independent dynamics, persistence, resistance, and rapid, threshold-like reorganization (in a geological time frame).

In Table 1, I have attempted to summarize the hierarchical pattern of organization and to tie various terms to it; I admit that cross-correlation of the terminology was difficult and not always obvious.

TABLE 1. Terminology and ecological pattern. Underlined terms are meant to describe formally the temporal counterparts of a spatial hierarchy. Rather than recognize separate temporal and spatial hierarchies, I have chosen to use the spatial nomenclature as a baseline and examine the temporal dynamics of these more familiar units of organization.

Modern ecology	Plant paleoecology	Invertebrate paleoecology*
Guild	Ecomorph/ guild	Guild
Community	Species assemblage	Biofaces/recurrent assemblage
Landscape	Landscape	Ecological–evolutionary subunit
Biome	Biome	?Ecological–evolutionary unit
Province	Province	Province

* Invertebrate paleoecological terminology is from Brett et al. (1990) and Brett and Baird in press.

Individualistic Dynamics and Questions of Scale

Prevailing reductionist views in neoecology must be reconciled with long-term patterns from truly ancient ecosystems. If individualistic models can be extrapolated to explain patterns at all spatial and temporal scales, then species assemblages and landscape patterns must have been continually reassembled after regional disruptions. Such models do not make reconciliation between neo- and paleoecology easier, and in fact may require many more ad hoc assumptions (about climate, geography, migration rates, and deterministic mechanisms of species assembly) than would hierarchical models.

Where do individualist dynamics fit in? The marine and terrestrial records suggest that species prefer a limited range of physical environmental conditions. When viewed on short time scales, such preferences appear to be prima facie evidence for species individualism, and indeed such explanations accurately capture patterns at certain times in the geological record. Yet, when viewed on long time scales, patterns at several organizational levels reappear over and over through millions of years. There also is evidence that the species composition of communities strongly limits the patterns of turnover and contributes to invasion resistance at several levels of organization, what Pimm (1991) calls "home field advantage." Perhaps individualism is limited by mutualistic interactions evolved during times when extinction levels are low. On the other hand, paleontological data strongly suggest that during times of high species extinction the fabric of species assemblages breaks down and causes disruption of higher order structure. During such times individualistic dynamics may be the general rule until a new system of ordered dynamics is established. Could the Recent be a time period of dominantly Gleasonian, individualistic dynamics, not characteristics of most of geological time? Has there been a progressive trend toward greater prevalence of individualistic dynamics through time? Can theory based on modern plants and animals adequately account for paleontological patterns? The answers to such questions may lie as much in broadening our expectations of the possible as in further data gathering and analysis.

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Literature Cited

Allen, T. F. H., and T. W. Hoekstra. 1992. Toward a unified ecology. Columbia University Press, New York.

Behrensmeyer, A. K., J. D. Damuth, W. A. DiMichele, R. Potts, H.-D. Sues, and S. L. Wing. 1992. Terrestrial ecosystems through time. University of Chicago Press.

Boucot, A. J. 1983. Does evolution take place in an ecological vacuum? Journal of Paleontology 57:1–30.

Brett, C. E., and G. C. Baird. In press. Coördinated stasis and evolutionary ecology of Silurian to Middle Devonian faunas in the Appalachian Basin. *In* D. Erwin, ed., New approaches to speciation in the fossil record. Columbia University Press, New York.

Brett, C. E., K. B. Miller, and G. C. Baird. 1990. A temporal hierarchy of paleoecological processes within a Middle Devonian epeiric sea. Pp. 178–209 *in* Miller 1990b.

Clements, F. E. 1916. Plant succession, an analysis of the development of vegetation. Publication No. 242, Carnegie Institution, Washington, D.C.

Cridland, A. A., and J. E. Morris. 1963. *Taeniopteris*, *Walchia*, and *Dichophyllum*, in the Pennsylvanian System of Kansas. University of Kansas Science Bulletin 44:71–85.

DiMichele, W. A., and R. B. Aronson. 1992. The Pennsylvanian-Permian vegetational transition: a terrestrial analogue to the onshore-offshore hypothesis. Evolution 46:807–824.

DiMichele, W. A., and T. L. Phillips. In press. The response of hierarchically-structured ecosystems to long-term climate change: a case study using tropical peat swamps of Pennsylvanian age. National Research Council, Geophysics Study Committee, Washington, D.C.

DiMichele, W. A., T. L. Phillips, and R. G. Olmstead. 1987. Opportunistic evolution: abiotic environmental stress and the fossil record of plants. Review of Palaeobotany and Palynology 50:151–178.

Gastaldo, R. A. 1987. Confirmation of Carboniferous clastic swamp communities. Nature (London) 326:869–871.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bulletin of the Torry Botanical Club 53:7–26.

Graham, R. W., and E. C. Grimm. 1990. Effects of global change on the patterns of terrestrial biological communities. Trends in Ecology and Evolution 5:289–292.

Miller, W., III. 1990a. Hierarchy, individuality and paleoecosystems. Pp. 31–47 *in* Miller 1990b.

———, ed. 1990b. Paleocommunity temporal dynamics: the long-term development of multispecies assemblages. Paleontological Society Special Publication No. 5. Lawrence, Kans.

———. 1993. Models of recurrent fossil assemblages. Lethaia 26:182–183.

Olson, E. C. 1985. Permo-Carboniferous vertebrate communities. Ninth International Congress of Carboniferous Stratigraphy and Geology, Comptes Rendus 5:331–345.

O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. A hierarchical concept of ecosystems. Monographs in Population Biology 23, Princeton University Press.

Overpeck, J. T., R. S. Webb, and T. Webb, III. 1992. Mapping eastern North American vegetation change of the past 18 ka: no-analogs and the future. Geology 20:1071–1074.

Pfefferkorn, H. W., and M. C. Thomson. 1982. Changes in dominance patterns in Upper Carboniferous plant-fossil assemblages. Geology 10:641–644.

Phillips, T. L., and R. A. Peppers. 1984. Changing patterns of Pennsylvanian coal-swamp vegetation and implications of climatic control on coal occurrence. International Journal of Coal Geology 3:205–255.

Pimm, S. L. 1991. The balance of nature? University of Chicago Press.

Raymond, A. 1993. Seeds, climate, and Middle Carboniferous land plant diversity. Geological Society of America, Abstracts with Programs, A-389.

Schubert, J. K., and D. J. Bottjer. 1993. Recovery from the end-Permian mass extinction event: paleoecology of Lower Triassic marine invertebrate assemblages in the Great Basin. Geological Society of America, Abstracts with Programs, A-156.

Sheehan, P. M. 1985. Reefs are not so different—they follow the evolutionary pattern of level-bottom communities. Geology 13:46–49.

Wing, S. L. 1984. Relation of paleovegetation to geometry and cyclicity of some fluvial carbonaceous deposits. Journal of Sedimentary Petrology 54:52–66.