

**SPOTLIGHT****SHORTENING THE GAP BETWEEN MODERN COMMUNITY ECOLOGY AND EVOLUTIONARY PALEOECOLOGY**

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Zeno of Elea, the ancient Greek philosopher, proposed a paradox that captures one of the challenges facing evolutionary paleoecologists: that which is in motion must arrive at the halfway stage before it arrives at its goal (Aristotle, 1984). Zeno describes a footrace between Achilles and a tortoise and explains that if Achilles, a fast runner, gives the tortoise a head start, he will never overtake the tortoise. Achilles must traverse a finite series of distances before catching the tortoise, but in the time it takes Achilles to achieve this distance the tortoise crawls forward a tiny bit farther. As a result, Achilles is forever chasing a tortoise he can never actually catch.

This seeming paradox resembles one of the challenges facing evolutionary paleoecologists; that is, the ever-present challenge of keeping up with developments in modern community ecology—a swift opponent with a definite head start. Several major patterns of functional biology and life habits are well established for marine organisms throughout the Phanerozoic (Bambach, 1985, 1993; Sepkoski and Miller, 1985; Bottjer and Ausich, 1986). The lack of coherent theories to help understand these macroevolutionary trends, however, keeps evolutionary paleoecology a step behind (Jackson, 1988; Allmon, 1994; Allmon and Bottjer, 2001). The good news is that this paradox is not irresolvable. Perhaps evolutionary paleoecologists, like the mathematicians who used calculus to produce practical solutions to Zeno's paradox, can use math to gain headway; for example, the mathematical model of the unified neutral theory of biodiversity and biogeography (Hubbell, 2001). The unified neutral theory might prove useful to paleontologists because it results in a large number of testable predictions concerning presence-absence, relative abundance, and persistence times of species in communities, as well as testable predictions about modes of speciation. What is most exciting is the ability of the theory to predict modes of speciation—before we can ask how ecological processes help mold evolution through time, we need to determine how species originate. For those not familiar with this theory, a brief overview is provided here, but details can be found in Hubbell's (2001) book, *The Unified Neutral Theory of Biodiversity and Biogeography*.

The unified neutral theory builds onto the well-known theory of island biogeography (MacArthur and Wilson, 1967) by incorporating a dynamic theory of relative species abundance and sets forth a synthetic explanation for the observed species abundance patterns within modern ecological communities (Hubbell, 2001, 2005; Chave, 2004). Similar to the theory of island biogeography, the unified neutral theory assumes that ecological equivalents have the same birth, death, and migration rates. Unlike the theory of island biogeography, however, the unified neutral theory defines this symmetry (i.e., neutrality) at the individual level rather than at the

species level; it is argued that the probability of speciation and extinction are dictated by relative abundance (Levinton, 1979; Hubbell, 2001). By incorporating speciation into the theory of island biogeography, the unified neutral theory is able to predict the existence of a fundamental biodiversity number, which determines the distribution of species richness and relative species abundance on a wide variety of spatial and temporal scales, an aspect that makes this theory appropriate for application to the fossil record (Hubbell, 2005). One of its significant predictions states that speciation mechanisms can be determined by examining macroevolutionary patterns of species richness and relative abundance patterns (Hubbell, 2005). If speciation mechanisms and these macroecological patterns are linked, as Hubbell (2001) suggests, then documenting relative species abundance in the fossil record will further our insight into speciation



Nicole Bonuso grew up in the Triassic of New Jersey but did not really fall in love with paleontology until the summer after earning her B.A. in Geology from the University of Rhode Island. She was encouraged by her undergraduate advisor, David Fastovsky, to spend the summer at Petrified Forest National Park in the hopes that she would get hooked on paleontology. It was a devious and ingenious plan, and it worked! After a year of grunt work at Lamont-Doherty, Nicole headed to Syracuse University for her Master's and then continued west to the University of Southern California for her Ph.D. Nicole is currently an assistant professor at California State University, Fullerton, where she continues to work on evolutionary paleoecological questions. Here she is pictured (left) with her friend Carrie Browne on top of Mount San Antonio, the highest peak in the San Gabriela Mountains of Southern California.

processes. If speciation processes can be determined, it will prove invaluable to helping researchers translate ecological interactions into macroevolutionary trends.

My primary goal in the coming years will be to try to incorporate the unified neutral theory into evolutionary paleoecology by examining local and regional relative abundance patterns within the Middle Triassic. The Middle Triassic is often overlooked because by this time speciation increases and so-called Lazarus taxa appear, marking the onset of ecosystem recovery (Jablonski, 1986; Erwin, 1996, 2006). Recent research indicates that Early Triassic survivors fail to persist beyond the Olenekian stage (last stage of the Early Triassic) and thus fall into the category referred to as Dead Clade Walking (Jablonski, 2002). It is not until the Anisian stage of the Middle Triassic that survival rates begin to increase to pre-extinction levels (Jablonski, 2002). It is generally understood that a major restructuring of marine organisms occurred after the end-Permian mass extinction in terms of ecological complexity and diversity dynamics (Vermeij, 1977; Sepkoski, 1981; Erwin, 1994, 1998, 1999; Miller and Foote, 2003; Wagner et al., 2006). If the Early Triassic survivors of the end-Permian mass extinction do not participate in postrecovery diversification, then the Middle Triassic holds the key to the origins of this major marine restructuring and warrants further study.

Despite the enormous progress over the past 30 years, the cause of the post-Paleozoic reorganization remains contentious. Several hypotheses have been proposed to explain the change from Paleozoic to post-Paleozoic marine ecosystems: changes in predation patterns, increasing disturbance of sessile benthos through bioturbation and rasping herbivores, and specific competition for resources—the most classic explanation (Rudwick, 1970; Steele-Petrovic, 1976; Thayer, 1981, 1983, 1985, 1986; Vermeij, 1987; Donovan and Gale, 1990; Rhodes and Thompson, 1993). Exploitation of new ecospace, diversity dependence, and species packing have also been used as explanations for the replacement process (Sepkoski, 1979; Bambach, 1985; Sepkoski and Miller, 1985; Bottjer and Ausich, 1986; Miller and Sepkoski, 1988), as well as a change to a more nutrient-rich sea, leading to greater availability of food resources (Vermeij, 1987; Bambach, 1993, 1999).

Can the unified neutral theory help us provide fundamental insight into post-Paleozoic marine ecological changes? I believe it has heuristic power through its inherent links to determining speciation processes, and what better place to test this method than in the Middle Triassic, the time when many post-Paleozoic marine taxa originated.

## REFERENCES

- ALLMON, W.D., 1994, Taxic evolutionary paleoecology and the ecological context of macroevolutionary change: *Evolutionary Ecology*, v. 8, p. 95–112.
- ALLMON, W.D., and BOTTJER, D.J., 2001, Evolutionary paleoecology: The maturation of a discipline, in Allmon, W.D., and Bottjer, D.J., eds., *Evolutionary Paleoeology: The Ecological Context of Macroevolutionary Change*: Columbia University Press, New York, p. 1–8.
- ARISTOTLE, 1984, *Physics*, in Barnes, J., ed., *The complete works of Aristotle: The revised Oxford translation*: Princeton, Princeton University Press, p. 2,512.
- BAMBACH, R.K., 1985, Classes and adaptive variety: The ecology of diversification in marine faunas through the Phanerozoic, in Valentine, J.W., ed., *Phanerozoic Diversity Patterns: Profiles in Macroevolution*: Princeton University Press, New Jersey and Pacific Division, American Association for the Advancement of Science, San Francisco, p. 191–253.
- BAMBACH, R.K., 1993, Seafood through time: Changes in biomass, energetics, and productivity in the marine ecosystem: *Paleobiology*, v. 19, p. 372–397.
- BAMBACH, R.K., 1999, Energetics in the global marine fauna: A connection between terrestrial diversification and change in the marine biosphere: *Géobios*, v. 32, p. 131–144.
- BOTTJER, D.J., and AUSICH, W.I., 1986, Phanerozoic development of tiering in soft substrata suspension-feeding communities: *Paleobiology*, v. 12, p. 400–420.
- CHAVE, J., 2004, Neutral theory and community ecology: *Ecology Letters*, v. 7, p. 241–253.
- DONOVAN, S.K., and GALE, A.S., 1990, Predatory asteroids and the decline of the articulate brachiopods: *Lethaia*, v. 23, p. 77–86.
- ERWIN, D.H., 1994, The Permo-Triassic extinction: *Nature*, v. 367, p. 231–236.
- ERWIN, D.H., 1998, The end and the beginning: Recoveries from the mass extinctions: *Trends in Ecology and Evolution*, v. 13, p. 344–349.
- ERWIN, D.H., 1999, Biotic recoveries from mass extinctions: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 154, p. 1–132.
- HUBBELL, S.P., 2001, *The Unified Neutral Theory of Biodiversity and Biogeography*: Princeton University Press, Princeton, New Jersey, 375 p.
- HUBBELL, S.P., 2005, The neutral theory of biodiversity and biogeography and Stephen Jay Gould: *Paleobiology*, v. 31, p. 122–132.
- JABLONSKI, D., 2002, Survival without recovery after mass extinctions: *Proceedings of the National Academy of Sciences*, v. 99, p. 8,139–8,144.
- JACKSON, J.B.C., 1988, Does ecology matter? Review of *Evolution and Escalation: An Ecological History of Life* by G.J. Vermeij: *Paleobiology*, v. 14, p. 307–312.
- LEVINTON, J.S., 1979, A theory of diversity equilibrium and morphological evolution: *Science*, v. 204, p. 335–336.
- MACARTHUR, R.H., and WILSON, E.O., 1967, *The Theory of Island Biogeography*: Princeton University Press, Princeton, New Jersey, 203 p.
- MILLER, A.I., and FOOTE, M., 2003, Increased longevity of post-Paleozoic marine genera after mass extinctions: *Science*, v. 302, p. 1,030–1,032.
- MILLER, A.I., and SEPKOSKI, J.J., JR., 1988, Modeling bivalve diversification: The effect of interaction on a macroevolutionary system: *Paleobiology*, v. 14, p. 364–369.
- RHODES, M.C., and THOMPSON, R.J., 1993, Comparative physiology of suspension-feeding in living brachiopods and bivalves: Evolutionary implications: *Paleobiology*, v. 19, p. 322–334.
- RUDWICK, M.J.S., 1970, *Living and Fossil Brachiopods*: Hutchinson University Library, London, 199 p.
- SEPKOSKI, J.J., JR., 1979, A kinetic model of Phanerozoic taxonomic diversity; II, Early Phanerozoic families and multiple equilibria: *Paleobiology*, v. 5, p. 222–251.
- SEPKOSKI, J.J., JR., 1981, A factor analytic description of the Phanerozoic marine record: *Paleobiology*, v. 7, p. 36–53.
- SEPKOSKI, J.J., JR., and MILLER, A.I., 1985, Evolutionary faunas and the distribution of Paleozoic marine communities in space and time, in Valentine, J.W., ed., *Phanerozoic Diversity Patterns: Profiles in Macroevolution*: Princeton University Press, Princeton, New Jersey, p. 153–190.
- STEELE-PETROVIC, H.M., 1976, Brachiopod food and feeding processes: *Palaeontology*, v. 19, p. 417–436.
- THAYER, C.W., 1981, Ecology of living brachiopods, in Dutro, J.T., Boardman, R.S., organizers, *Lophophorates: Notes for a Short Course*: University of Tennessee Department of Geological Studies, Studies in Geology, v. 5, p. 110–126.
- THAYER, C.W., 1983, Sediment-mediated biological disturbances and the evolution of marine benthos, in Tevesz, M.J.S., and McCall, P.L., eds., *Biotic Interactions in Recent and Fossil Benthic Communities*: Plenum, New York, p. 479–625.
- THAYER, C.W., 1985, Brachiopods versus mussels: Competition, predation and palatability: *Science*, v. 228, p. 1,527–1,528.
- THAYER, C.W., 1986, Are brachiopods better than bivalves? Mechanisms of turbidity tolerance and their interaction with feeding in articulates: *Paleobiology*, v. 12, p. 161–174.
- VERMEIJ, G.J., 1977, The Mesozoic marine revolution: Evidence from snails, predators, and grazers: *Paleobiology*, v. 3, p. 245–258.
- VERMEIJ, G.J., 1987, *Evolution and Escalation: An Ecological History of Life*: Princeton University Press, Princeton, New Jersey, 527 p.
- WAGNER, P.J., KOSNIK, M.A., and LIDGARD, S., 2006, Abundance distributions imply elevated complexity of post-Paleozoic marine ecosystems: *Science*, v. 314, p. 1,289–1,292.