Historical influences on community ecology

Harry W. Greene*
Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853

Why does California, a large and topographically complex state that spans fog-drenched redwood groves to desert sand dunes, have 30 species of snakes, whereas roughly twice that number occur in five square miles of lowland Costa Rican rainforest? Almost 400 species of birds, a bit more than half as many as breed in the entire continental United States, occupy that same small Central American site, and indeed, all over the world, most groups of organisms increase in species richness as one moves from the poles toward the equator. Lifestyle diversity also varies globally, and increased numbers of species often reflect primarily ecological diversification; most temperate-zone bats feed on insects, for example, whereas tropical chiropteran faunas include specialists on fruit, nectar, fish, frogs, birds, and blood. Finally, biological diversity can vary extensively and exclusive of latitude, among grossly similar habitats: lizards reach a maximum of ≈15–20 species at North American desert sites, whereas several times that many species occur at some Australian desert localities. Such dramatic global variation has intrigued naturalists for centuries, and even now its causes are only partly understood. Most conceptual and empirical work in 20th century community ecology focused on contemporary processes, whereas an article by Vitt and Pianka (1) in a recent issue of PNAS demonstrates that dietary relationships in modern lizard assemblages may, in large measure, reflect the evolutionary origins of a few morphological and behavioral novelties during the Mesozoic, >100,000,000 years ago.

Causes of Diversity

With respect to understanding the upper limits of species diversity, rainforests occupy huge expanses of equatorial Africa, Asia, and the New World, so the biologically most opulent places on Earth are generally hot and wet. Over evolutionary time, rising sea levels and tectonic events have fragmented landscapes and populations, thereby catalyzing speciation. More land, more sun, and more rain, coupled with geographical isolation of habitats, have thus led to more kinds of plants, more kinds of insects that eat plants, more kinds of frogs that eat insects, more kinds of snakes that eat frogs, and more kinds of birds and mammals that eat arthropods, amphibians, reptiles, and each other. On more local spatial scales, chunks of tropical forest are chronically annihilated by earthquakes, volcanic activity, and windstorms, then colonized with species that live in the resulting "light gaps," and forest inhabitants eventually again replace those sun-loving newcomers. These cycles of disturbance increase overall regional diversity by generating patchworks of early and late succession-stage organisms in what might otherwise have been an unbroken expanse of rainforest. Within individual habitat types, in tropical forests as well as in deserts and other simpler ecosystems, coexisting closely related species typically differ in diet and/or other aspects of resource utilization.

Vitt and Pianka's analyses revealed significant dietary shifts at six major divergence points.

The explanatory scheme I have just briefly summarized is multifactorial and alludes to a role for history, but until recently most ecologists have focused instead on contemporary determinants of community composition, in particular food and microhabitat availability, competition, predation, and local disturbance (2). Accordingly, a common research program in the 1970s and 1980s was to explore patterns of niche breadth and niche overlap within and among taxonomic assemblages (e.g., grassland birds and desert lizards), with the expectation that more complex communities would exhibit predictable patterns on the basis of competition theory (3). A shift in emphasis was presaged by Brooks' (4) explicit conceptual linkage of ecology with evolutionary history and by Brooks and McLennan's (5) pioneering theoretical overview. During the ensuing two decades, phylogenetic effects on community structure have been recognized for organisms as different as crustaceans (6), damselflies (7), turtles (8), and snakes (9), usually among those that have diverged relatively recently within a single continent or on contiguous land masses.

Now Vitt and Pianka (1) provide strong evidence for dramatic historical effects on contemporary ecological community structure, based on an unusually broadly sampled, ancient, and worldwide adaptive radiation. They assembled extensive dietary data for 184 species from 12 families of lizards, collected in diverse habitats on four continents, then divided all prey into 27 categories (12 categories accounted for ≈90% of all food items). Using a consensus of lizard phylogenies to reconstruct the evolutionary history of the included taxa and mean species body size as a covariate, they then used a multivariate ordination procedure to statistically associate variation in lizard diets with evolutionary diversification.

Vitt and Pianka's (1) analyses revealed significant dietary shifts at six major divergence points within the evolutionary history of lizards, collectively accounting for ≈80% of the variance in diet composition among the species sampled. About 28% of the total variance was explained by the first and most obvious dietary divergence, between Iguania (iguanids, agamids, and chameleons) and Scleroglossa (geckos, skinks, monitors, and other lizards as well as amphisbaenians and snakes); this divergence occurred in the late Triassic and was concordant with a major dichotomy in functional morphology, behavior, and ecology. Iguanians generally retain primitive lepidosaurian biology, whereas scleroglossans exhibit shared derived transitions that include lingual to jaw prehension of food, increased reliance on chemical cues, and a more active foraging mode. Iguanians feed on large numbers of visually detected ants, other hymenopterans, and beetles, whereas scleroglossans often eat primarily termites, immature life stages, and prey that are otherwise immobile and/or hidden. A recent molecular phylogenetic study challenged some aspects of squamate phylogenetic orthodoxy (10), but Vitt and Pianka confirmed their most important results with a reanalysis using the alternative divergence topology.

Future Prospects

Several more recent conceptual overviews (8, 11–14) have revised and

See companion article on page 7877 in issue 22 of volume 102.

*E-mail: hwg5@cornell.edu.

© 2005 by The National Academy of Sciences of the USA

extended Brooks and McLennan's (5) original exploration of the relationships between history and contemporary factors in structuring ecological communities, and future progress will depend in part on a wider range of empirical studies. Vitt and Pianka (1) emphasized that historical and contemporary determinants are likely hierarchical rather than antithetical, and their demonstration of multiple significant association at various deep levels within lizard phylogeny, coupled with evidence that a particular lineage of temperate South American iguanians has repeatedly evolved herbivory (15), is consistent with theoretical expectations that macroevolutionary trends scale up from microevolutionary processes (16).

Three related aspects of Vitt and Pianka's (1) study deserve emphasis with respect to more general issues. First, the patterns they describe entail the influence of fundamentally organismal- and population-level properties on community-level patterns; after all, the most profound dietary divergence among squamate reptiles was originally elucidated by Schwenk's dissertation research on the comparative anatomy of lizard tongues (17). Second, Vitt and Pianka's data set has few, if any, published equals in terms of taxonomic complexity and geographical breadth, and, as they note, assembling it occupied the better parts of two academic careers (their specimens with stomach contents are curated in public museum collections, available for further research by qualified investigators). Widespread application of comparable phylogenetic approaches to community ecology would require an enormous increase in available natural history data, as well as the relevant phylogenies. Third, whatever roles history may prove to have played in the ecology of particular communities, those effects will likely have ramified even more broadly and thus warrant attention in ecosystem-level studies and efforts to conserve biodiversity (18). Collectively, these points underscore Bartholomew's (19) dictum that phenomena at a particular level of biological organization depend on mechanisms at lower levels yet often find their greatest significance at higher levels.

In the first few decades of the 21st century, more than ever before, we face the prospect of a seamless integration across all of biology. With the recent rise of genomics, linkages between development and evolution, and phylogenetics, the life sciences are poised for an unprecedented conceptual unification, one that can range back and forth from molecules to the entire biosphere. The potential for thereby addressing emerging infectious diseases, introduced species, habitat fragmentation, and other serious problems is correspondingly encouraging. Organisms themselves are at the center of the hierarchy of biological complexity (20), and our challenge now is to forge support for all sectors of this truly integrative and comparative vision.

1. Vitt, L. J. & Pianka, E. R. (2005) *Proc. Natl. Acad. Sci. USA* **102**, 7877–7881.
2. Schoener, T. W. (1977) in *Biology of the Reptilia*, eds. Gans, C. & Tinkle, D. W. (Academic, New York), pp. 35–136.
3. Pianka, E. R. (1986) *Ecology and Natural History of Desert Lizards: Analyses of the Ecological Niche and Community Structure* (Princeton Univ. Press, Princeton).
4. Brooks, D. R. (1985) *Ann. Mo. Bot. Gard.* **72,** 660–680.
5. Brooks, D. R. & McLennan, D. A. (1991) *Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology* (Univ. Chicago Press, Chicago).
6. Hairston, N. G., Jr., & Cáceres, C. E. (1996) *Hydrobiologia* **320,** 27–44.
7. McPeek, M. A. & Brown, J. M. (2000) *Ecology* **81,** 904–920.
8. Stephens, P. R. & Wiens, J. J. (2004) *Am. Nat.* **164,** 244–254.
9. Cadle, J. E. & Greene, H. W. (1993) in *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, eds. Ricklefs, R. E. & Schluter, D. (Univ. Chicago Press, Chicago), pp. 281–293.
10. Townsend, T. M., Larson, A., Louis, E. & Macey, J. R. (2004) *Syst. Biol.* **53,** 745–757.
11. Losos, J. B. (1996) *Ecology* **77,** 1344–1354.
12. Brooks, D. R. & McLennan, D. A. (2002) *The Nature of Diversity: An Evolutionary Voyage of Discovery* (Univ. Chicago Press, Chicago).
13. Campbell, O. W., Ackerly, D. D., McPeek, M. A. & Donoghue, M. J. (2002) *Annu. Rev. Ecol. Syst.* **33,** 475–505.
14. Wiens, J. J. & Donoghue, M. J. (2004) *Trends Ecol. Evol.* **19,** 639–644.
15. Espinoza, R. J., Wiens, J. J. & Tracy, C. R. (2004) *Proc. Natl. Acad. Sci. USA* **101,** 16819–16824.
16. Arnold, S. J., Pfrender, M. E. & Jones, A. G. (2001) *Genetics* **112–113,** 9–32.
17. Schwenk, K. & Throckmorton, G. S. (1989) *J. Zool. (London)* **219,** 153–175.
18. Donlan, C. J. & Martin, P. S. (2004) *Conserv. Biol.* **18,** 267–269.
19. Bartholomew, G. A. (1964) *Symp. Soc. Exp. Biol.* **18,** 7–29.
20. Greene, H. W. (2005) *Trends Ecol. Evol.* **20,** 23–27.