BOOK REVIEWS

The Ecology of Coexistence

Species Diversity in Ecological Communities. Historical and Geographical Perspectives. ROBERT E. RICKLEFS and DOLPH SCHLUTER, Eds. University of Chicago Press, Chicago, 1994. viii, 414 pp., illus. $98 or £78.50; paper, $32.50 or £25.95.

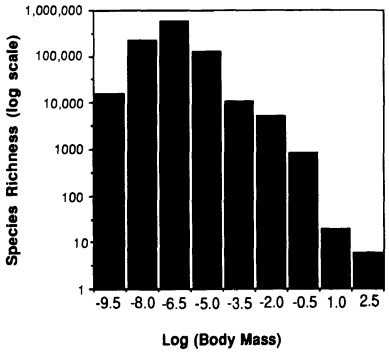
In 1959, in a thoughtful essay entitled "Homage to Santa Rosalia, or why are there so many kinds of animals?" G. E. Hutchinson set much of the agenda for the next several decades of community ecology. Not only did Hutchinson focus attention on the ecological processes that enable species to coexist in the same environment, he was remarkably prescient: most of the processes that he hypothesized to be important in regulating diversity are still the subjects of major research programs today.

Now, 35 years after Hutchinson's 14-page essay, we have a wonderful 414-page volume summarizing the extent to which modern ecology has succeeded in explaining biological diversity. Ricklefs and Schluter have put together a compendium of 30 chapters by 50 authors from 10 countries that provides an exceptionally broad and deep representation of the current state of the science. There are few senior community ecologists, kinds of organisms and habitats, or approaches to the subject that are not represented. There is such a wealth of ideas and information that in my department we plan to spend the entire coming semester of our journal club on the volume. I suspect many other seminar groups will want to do likewise.

To the extent that I have been able to assimilate its material so far, I find that the book does two important things. First, it shows how much we have learned about the organization and diversity of ecological communities in the last 35 years. A careful reading should make it clear, even to the skeptics, that contemporary ecology is built upon a strong empirical and theoretical foundation.

Many chapters present and analyze data of impressive quantity and variety, representing a wide range of temporal and spatial scales. There are intensive studies of herbivore-plant and parasite-host communities (Cornell; Farrell and Mitter; Aho and Bush; Lawton *et al.*; Brooks and McLennan), comparative analyses of multiple assemblages within geographic regions (Cody; Morton), comparisons between islands and mainlands (Blondel and Vigne) and among continents (Westoby; Ricklefs and Latham; Cadle and Green) and oceans (McGowan and Walker), and syntheses of 600 million years of fossil evidence of the history of organic diversity (Kauffman and Fagerstrom; Van Valkenburgh and Janis; Valentine and Jablonski). There is now a wealth of sound data, not only on the patterns of diversity at different temporal and spatial scales but also on the processes that influence the number and identities of species in these assemblages.

These empirical studies use a variety of methods and approaches, including controlled, replicated experiments (Underwood and Petraitis), comparative, nonmanipulative field studies (most of the authors mentioned above), and analyses of large, computerized databases compiled from many sources (Pearson and Juliano, Schluter and Ricklefs, Latham and Ricklefs). The diversity of non-experimental studies is a healthy sign. For too long ecology has suffered from a preconception that the only way to do rigorous empirical research is to perform manipulative experiments. The resulting small-scale, short-term studies simply cannot adequately address many of the important questions raised in this volume.



"Preliminary data gathered by [Robert] May (1978, 1986) on the relationship between the total number of animal species on earth and their body size. May expressed size as length, L. To prepare this figure, May's estimates were converted to body mass using the assumption that mass is proportional to L^3. A simple regression of log(species richness) on log(body mass), using the seven data points on the declining portion of this figure, led to an estimated slope of −0.56. All these numbers are extremely preliminary, and should serve, we hope, to encourage a more rigorous collection and synthesis of such data." [From D. Tilman and S. Pacala's chapter in *Species Diversity in Ecological Communities*]

Ecology has also seen the development of a substantial body of theory. A wealth of mathematical and computer models have been used to analyze the logical consequences of many kinds of interactions. These efforts are well represented in the book in chapters on interspecific interactions (Tilman and Pacala; Yodzis; McLaughlin and Roughgarden), relationships between local and regional processes (Holt; Caswell and Cohen; Hanski *et al.*), and simulated insular biogeography (Haydon *et al.*). An encouraging sign in these chapters is the movement away from simplistic, pairwise models of interspecific interactions to more realistic formulations that consider multiple species and incorporate environmental heterogeneity.

The second thing this book does is to make clear that modern ecology still has no general, satisfying answer to Hutchinson's question. There is still no consensus on how to explain the most pervasive patterns of biological diversity—the variation in number of species with latitude, elevation, and ocean depth. This is illustrated by two chapters (Rosenzweig and Abramsky; Wright *et al.*) that discuss the relationship between diversity and productivity and reach quite different conclusions. It is also illustrated by the overall theme of the book: that traditional ecological studies of local patterns and processes are inadequate to understand diversity; it is necessary to add a geographical and historical perspective. The editors make their case in part by including chapters by biogeographers, paleobiologists, and systematists. These give the book an exceptional breadth of data, theory, and viewpoint. They also illustrate how many different kinds of phenomena must be considered to understand the distribution and variety of life on Earth.

It is almost as if the more we have learned, the more difficult it has become to answer Hutchinson's question. In the 1960s and 1970s most community ecologists were interested primarily in the influence of biotic interactions on local community structure. We realized that the abiotic environment, geographic processes, and historical events were also important, but we usually designed our models, experiments, and comparative studies so as to hold these influences constant and focus on local phenomena. Now we are beginning to realize that this approach is not working. The effects of the physical, geographic, and historical processes are so pervasive that they cannot be ignored. But it is not clear how to incorporate the effects of biogeochemical ecosystem

processes, earth history, phylogenetic constraints, and species dynamics (speciation, colonization, and extinction) in a way that clarifies, rather than complicates, the issue of diversity.

One thing that this book does not do is offer much in the way of suggestions of how to deal with all the complexity it documents. This is a matter of the current state of community ecology, and the intent of bringing together so many authors was clearly to illustrate the scope of the problem rather than to achieve a consensus about the direction of future research. But the question remains, Where do we go from here in our efforts to answer Hutchinson's question? If there is to be substantive progress, I think it will involve major changes in the way we conduct ecological research. The ecology of the last several decades has been largely reductionist, striving to understand ecological systems by reducing their complexity. In my opinion, this approach is not working, or at least, is inadequate by itself. We must develop more holistic approaches that confront complexity directly. Some of the contributors to this volume (for example, Wright *et al.*; Holt; Haydon *et al.*; Farrell and Mitter; Brooks and McLennan) seem to be striking out in promising new directions. I will present some of my own ideas on the problem of ecological complexity in a forthcoming monograph (*Macroecology*, University of Chicago Press).

Many scientists in other disciplines still think of ecology as old-fashioned natural history or as comparable in rigor to a social science. Some ecologists, both young and old, are hypercritical and discouraged, rather than optimistic and excited, about the status and prospects of their discipline. I wish that all of these skeptics would read this book. It is a testament to how far ecology has come in the last 35 years and to the great challenges that still lie ahead.

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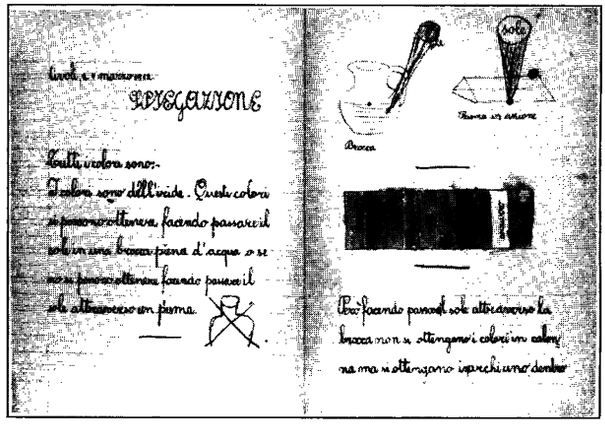
Days in Rome and Berkeley

A Mind Always in Motion. The Autobiography of EMILIO SEGRÈ. University of California Press, Berkeley, 1993. xii, 332 pp. + plates. $30 or £25.

The name of the late Emilio Segrè is perhaps most widely associated with the researches on neutron physics conducted under the guidance of Enrico Fermi in Rome in the early 1930s, when the myth of "the boys of Via Panisperna" was established, and with the Nobel Prize awarded to him some 20 years later for the discovery of the antiproton in Berkeley. These events of his career span two different times of physics, epitomizing the transition from "little" to "big" science, from the "string and sealing wax" handicraft of the Rome days to the big accelerator in the West Coast laboratory; and, more than that, two geographical sites deeply associated with different, often conflicting cultures.



Notebook of Emilio Segrè at age seven. "All the colors are: The colors are of the rainbow. These colors can be obtained by passing sunlight through a pitcher filled with water or by passing sunlight through a prism. However, by passing the sun through the pitcher one does not obtain the colors in columns but in arcs, one within [the other]." [From *A Mind Always in Motion*]

Like so many European scientists impelled to emigration by political events at home, Segrè had to find his way to adjust to the sudden transition between worlds, to maintain attachment to his roots while creating links with a second homeland. This book is largely the story of the working out of this tension. It is not a story written along the lines of a "scientific" autobiography; relatively little of it is devoted to strictly technical matters, the hard stuff always being kept to a bare minimum. Rather than on scientific deeds, the focus is on the milieu of the events and on the personalities of the actors. Throughout the book emerges Segrè's skill at evoking an atmosphere or sketching the characters of his colleagues. The author openly says that he has "not sought to display manners and tact I never had." The result is a lively gallery of portraits, in particular when we are offered Segrè's impressions of the Berkeley environment and the physicists there: Ernest Lawrence, "more a doer than a thinker . . . fundamentally generous and magnanimous" but "occasionally petty" and "childish" in his quest for power; Glenn Seaborg, whose "unbridled ambition" made him "determined to get ahead by any means"; Robert Oppenheimer, the "demigod" delighting in "erudite complexities," who nonetheless "knew quantum mechanics well, and in this was unique at Berkeley."

The only regret felt by the reader of these commentaries is that too often Segrè's remarks on his world are as superficial as caustic and incisive, and the exposition turns suddenly from an introspective approach that might shed new light to the pragmatic, matter-of-fact style that is the dominant tone of the narrative. It is quite clear, for example, that Segrè's relation with Berkeley's Radiation Laboratory was not exactly an idyll and that he had strong feelings about Edwin McMillan and Seaborg's 1951 Nobel Prize for chemistry as a recognition he deserved to share. That these and other issues are only hinted at is at times disappointing, considering that, for example, Segrè played a not minor part in the final stage of the construction of the atomic bomb as one of the leading scientists present at Los Alamos. His account of the days on the "fateful Mesa" is lively and rich in anecdotes and portraits, but very little emerges of the deeper motivations and conflicts that stirred the scientists in the laboratory. The ethical dilemmas and inner struggles that accompanied the "loss of innocence" of the physicists' community are given altogether less consideration in the book than is litigation concerning the family business in

"Franco Rasetti (nicknamed 'Cardinal Vicar'), Enrico Fermi ('Pope'), and Emilio Segrè ('Basilisk') in academic dress, 1931." [From *A Mind Always in Motion*]