The Refuge Theory

Biological Diversification in the Tropics. Proceedings of a symposium, Caracas, Venezuela, Feb. 1979. GHILLEAN T. PRANCE, Ed. Columbia University Press, New York, 1982. xvi, 714 pp., illus. $60.

Until the 1960's, the idea that the Neotropical lowland rain forests had been unaffected by the climatic deterioration of the Cenozoic was accepted by most biologists. In fact, this stability was often used as an explanation for their high species diversity. Beginning about 1969, the idea that lowland areas experienced Pleistocene climatic changes began to percolate into the scientific literature. The original biological studies were based on analyses of differentiation patterns of birds by Haffer and *Anolis* by Vanzolini and Williams. These authors concluded that the biotic patterns they observed resulted from Pleistocene arid cycles that fragmented the lowland rain forest and restricted forest-loving organisms to moist refuges in which divergence occurred. This idea has subsequently become known as the "refuge theory" and has recently been invoked by many workers as the major explanation for the generation of species in lowland tropical rain forests. It is not surprising, therefore, that the refuge theory was the theme of the fifth international symposium of the Association for Tropical Biology, or that the papers presented at the meeting have been gathered together into a book. It is somewhat surprising, in view of the limited scope of the book, that the title is *Biological Diversification in the Tropics*. However, Prance's introduction in part 1 properly focuses the book. The only other chapter in this part is one by Haffer summarizing the main kinds of evidence used to support the theory. Part 2 consists of six chapters that present geomorphological and palynological data indicating arid periods and suggesting restrictions of tropical forests during the last 2.5 million years. The chapter by Ab'Sáber is especially welcome because his work on stone lines has been a major source of evidence for former periods of aridity. Part 3 is a collection of seven chapters summarizing studies of plant groups that appear to reflect a history of isolation, differentiation, and re-expansion. Parts 4, 5, and 6 contain similar studies on insects, vertebrates, and primates, including humans. The seventh part presents the only papers (four) that deal with the Paleotropics. The final, eighth, part is a hodgepodge of papers on "theoretical and practical" aspects of the theory. These include alternatives to the refuge theory (Benson, Endler), theoretical hypotheses as to why refuge sizes might differ between taxa (Oren), and possible applications of the theory to conservation practices (Terborgh and Winter, Myers, Lovejoy).

Throughout the book, most of the botanists and zoologists (11 of 17) try to show how their data fit the theory or how the theory can explain the taxonomic and geographical patterns they observe in their organisms. The botanists (Toledo, Gentry, Prance, Granville, Steyermark) tend to draw conclusions from generalized distribution maps, a practice that can often lead to overly simplified interpretations, as Prance, Huber, and Brown emphasize. The interesting paper by Huber on savanna vegetation of Amazonian Venezuela shows how an understanding of the ecology and evolutionary origins of floristic elements can refine phytogeographical interpretations. Huber postulates that there are two kinds of savannas, only one of which may represent fragments of a former, more continuous, expanse of semiarid vegetation. The vertebrate zoologists, using a variety of techniques, come to varying conclusions. Duellman employs a vicariance approach to create somewhat forced historical sequences for anuran genera. Weitzman and Weitzman simply conclude that data on freshwater fish are not adequate for such reconstructions. Heyer and Maxson use a combination of morphological and chemical data as evidence for primary divergence of frogs in the Tertiary, rather than in the Pleistocene.

Some of the most stimulating discussions are presented by the three lepidopterists working with *Heliconius*, probably the best known biologically of any Neotropical genus. Despite the fact that they work with the same group of organisms, the three do not agree as to the mechanisms that have caused the proliferation of color forms present in species of the genus. Brown shows that areas of endemism in *Heliconius* do not correspond to areas of highest diversity. Endemism seems to be correlated with isolation in refuges and high diversity with high ecological heterogeneity, contact between regional faunas, or both. It is in this fine chapter that the poor printing of the volume is most frustrating, because it is difficult to distinguish between the butterfly morphs illustrated, and the many original maps of rainfall, soil types, and vegetation lose much of their detail. In other places in the book, the thinness of the paper is annoying because the print from the reverse side of a page is visible on the page being read.

Turner proposes that the proliferation of *Heliconius* mimetic variants was caused by differential extinction of color forms in refugia leading to different selective pressures for new arrays of color morphs. Benson differs with his colleagues and proposes some sort of parapatric divergence as the principal cause of the differentiation in *Heliconius*. This last idea is extended by Endler, who asserts that the patterns we now see can as easily be explained by a parapatric as by a refuge model. However, he then somewhat cavalierly says that one can easily invoke any theory that conforms to one's personal biases. To this last statement I take exception. If there were arid and wet cycles in lowland tropical regions during the last few million years, they must have affected the biotas. One of the exciting things about the book is that it shows that it is still necessary to prove that such periods did exist. There is at present no compelling evidence for a series of Pleistocene wet-arid cycles in lowland (as opposed to high montane, for which there is evidence) regions. Ab'Sáber finds remnants of only a Würm-Wisconsin cycle and of several short, minor Holocene dry periods. These latter may have had some effect on human populations and have led to the linguistic patterns explained in the chapters by Meggers and Migliazza. Though never mentioned in the book, there are geologists who interpret the Brazilian evidence differently from Bigarella, Andrade-Lima, and Ab'Sáber. Klammer (*Z. Geomorphol.* **25**, 146 [1981]), for example, adamantly argues that there was only a single, Cenozoic, dry episode and subsequent to that only minor Holocene dry intervals.

Even when, or if, the existence of wet-arid cycles is established on geoscientific evidence, the task of showing how organisms were affected remains. Livingstone wryly reminds us of the 20-year-long search for the location of the (now apparently illusory) Eastern Mixed-Mesophytic Forest Pleistocene refuge. Nev-

ertheless, many biologists have begun to assert with facility that isolation in Pleistocene forest refuges was a primary cause of lowland tropical species diversity. Such an unquestioned acceptance does not yet seem warranted. It is important to remember that the original studies were at the taxonomic level of superspecies or below. Haffer has been careful to point out that Pleistocene events caused extinctions as well as differentiation. Tropical rain forests were biologically diverse before the Pleistocene. There may have been no net change in the number of species over the last few million years. The major effect of climatic fluctuations may have been to alter distributions of species and to cause intraspecific differentiation rather than speciation.

As a whole, the volume is engrossing and mandatory reading for students of the Neotropics. Many of the studies have heretofore been published only as theses or technical bulletins (for example, Lamas, Toledo) or in journals that are difficult to obtain in the United States (Ab'Sáber). The authors themselves and the data they present point out the strong and weak points of the refuge theory and the need for more geological and biological work bearing on it. Prance is to be commended for his fine editing and for allowing the tropics to be revealed to be as enigmatic as ever.

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Chilopoda

The Biology of Centipedes. J. G. E. LEWIS. Cambridge University Press, New York, 1981. viii, 476 pp., illus. $69.95

Although most animals are basically mobile digestive systems, I can think of no organism whose structural plan is more dominated by the front end than centipedes. The head is often the broadest part of the body, and if the actual mouthparts are of modest size they are overcompensated by a pair of formidable poison fangs modified from the first pair of legs (unique in the animal kingdom), and the entire muscular and flexible creature strikes even the most dispassionate observer as the epitome of frenetic rapacity (an impression abundantly confirmed by its behavior).

Looking beyond this unpromising facade, one finds that centipedes are at once among the most fascinating and least known of all animals. Like many other residents of the soil and litter milieux, they have been neglected by all but a few investigators, and what has been published on them has generally been widely scattered through a polyglot literature. The last general survey of centipede biology appeared nearly six decades ago and has long been obsolete. Unquestionably the lack of a modern authoritative synthesis has been the major deterrent to potential investigators of chilopods, and it is gratifying that this obstacle has now been removed by an internationally respected specialist on these animals.

The Biology of Centipedes follows a traditional organization, treating anatomy, function, behavior, ecology, and systematics in 24 chapters. The author has carefully selected and balanced the subject matter and illustrations. Moreover, his writing style is pleasant. Under each major subject heading the condition is covered in centipedes generally and then for each of the four orders. There is a bibliography of 561 references cited in the text.

One expects centipedes to be somewhat outlandish, but even having some familiarity with the group I found myself repeatedly astonished by Lewis's accounts of their structure, function, and general life-styles. What intriguing animals, and how little is actually known about them! Nearly every page repeats the admission that we are seeing only bits and pieces of a grand pattern. Here is a large group (an arthropod class with over 2500 known species) in which the taxonomy remains chaotic (even the families are not adequately defined), much of the simplest gross anatomy unstudied (let alone its macromolecules), and almost all information about its natural history anecdotal. If ever a group cried out for study on all fronts, it must be the Chilopoda. Whatever the past difficulties with literature may have been, Lewis's book now provides an elegant prelude for a more mature stage of chilopodology.

A critic may be forgiven for wishing to see more of a good thing. If I had jurisdiction over the second edition, I would propose the following changes: adoption of a smaller type size and more compact format, which would yield up to 20 percent more space for text without increasing pagination or decreasing readability; the addition of an introductory chapter on the history of chilopod study and another on biogeographic patterns; and last, but of foremost importance, expansion of the three chapters on systematics. The author states that the inadequate state of the group's taxonomy justifies only superficial treatment, but the same argument could have been used in the case of the other chapters as well. What better place to present a synopsis of the current classification of all supraspecific taxa than in a general reference work? A brief diagnosis for each family or subfamily, with a list of published generic names and pertinent literature, would have given aspiring students access to this difficult subject and placed its coverage on a basis equivalent with the other aspects of the group's biology.

En fin: there can no longer be any justification for any graduate student to pick away at fruit flies, milkweed bugs, and marine invertebrates, splitting molecules and inventing bizarre experiments in an attempt to wring yet another dribble of information from these already exploited creatures. Lewis's book provides a wide-open field for exploration, with a megaproblem per page, and fascinating problems at that, whether one's bent is holistic or molecular, experimental or systematic.

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Circannual Rhythms

Biological Clocks in Seasonal Reproductive Cycles. Proceedings of a symposium, Bristol, England, March 1980. B. K. FOLLETT and D. E. FOLLETT, Eds. Halsted (Wiley), New York, 1981. xii, 292 pp., illus. $49.95. Colston Papers, vol. 32.

Many organisms have seasonal reproductive cycles, presumably to ensure optimal conditions for the survival of offspring and to minimize the costs of maintaining the reproductive system during unfavorable conditions. However, such a strategy entails considerable risk, in that a single mistake in timing could prove extremely costly to entire populations. Thus it is hardly surprising that organisms have adopted a variety of strategies to prevent such mistakes. In many, although not all, cases, however, the seasonal change in daylength (photoperiod) serves as the most reliable and therefore most important signal for the initiation or termination of reproduction.

Most of the contributions in this volume offer reviews of progress since the 1960 Cold Spring Harbor symposium on biological clocks as well as some new empirical findings. The advances are characterized not so much by new ideas as by the elaboration and refinement of