Book Reviews

Community Ecology

Insects on Plants. Community Patterns and Mechanisms. D. R. STRONG, J. H. LAWTON, and RICHARD SOUTHWOOD. Harvard University Press, Cambridge, Mass., 1984. vi, 313 pp., illus. $35; paper, $18.95.

Community ecology is in a ferment, agitated by a rancorous debate about the degree of orderliness and the importance of competition in natural systems. Some of the disagreement is undoubtedly due to the disparate experiences of researchers working with different taxa. In this debate, studies of insects have stimulated many of the challenges to what some perceive to be a competition-biased, equilibrium-obsessed theory. Among insects, equilibria often are difficult to see and species interactions appear to be little affected by competition. These themes, and the additional question of the contribution of coevolution to plant-insect systems, are the focus of this provocative monograph. The authors are quick to point out that their concern with the community ecology of phytophagous insects is no esoteric hobby—after all, plants and their insect herbivores together represent one-half of all living species.

This is a wonderfully written, engaging book, with a very personal choice of examples. By emphasizing systems with which they themselves have worked (for example, *Spartina, Heliconia*, bracken fern, and British trees), the authors offer the insight that comes from a total of 65 years of studying plant-insect associations. *Insects on Plants* is also distinguished by an overriding conviction that populations are the basis of communities and that therefore an understanding of communities must proceed from an understanding of population ecology. Thus, to evaluate the relative importance of competition and predation, much attention is given to life table studies, *K*-factor analyses, and specific population responses to species manipulations. Little mention is made of community-wide, species-packing, or niche-partitioning patterns.

The authors fearlessly take stands on most of the major questions in community ecology as they apply to insect herbivores. They conclude that interspecific competition is feeble and sporadic in its effects but that natural enemies and interactions acting vertically in the food chain are important. The variable and unpredictable character of plant-insect associations is stridently documented and is assigned responsibility for what Strong has labeled "density-vague" population dynamics. We learn, however, that in spite of dramatic fluctuations in absolute densities the structure of the insect community on bracken fern has remained remarkably constant during an 11-year study by Lawton. (I would not expect this to hold up as a general result for insect communities.) Evidence for tight coevolution in plant-insect systems is found lacking—the authors argue that the scarcity of such evidence reflects the rareness of "the sustained, reciprocal and intense interactions that are necessary for coevolution" (p. 218). Additional topics include the evolution of insect diversity through geological time, the number of insect species that feed on particular host plants, consequences of plant defenses, and three-trophic-level interactions. These are all matters on which the authors have made major contributions in their own research.

My only complaint is that I think the authors are sometimes a bit uncritical in using the literature to support their arguments. For example, I do not think that Anderson and May's mathematical models show that natural cycles in the gray larch moth are "most likely" (table 5.2, p. 122) due to infectious disease; Anderson and May actually claim only that their models show that the cycles "may be" due to infectious diseases. Furthermore, the alluring qualitative verbal summaries of the effects of natural enemies and of plant defenses provided by the authors are not enough to satisfy me; I will tend to remain suspicious of our understanding until I see a mechanistic model that generates apt quantitative predictions about plant-herbivore-predator dynamics. Such quantitative theory is still in its infancy when it comes to plant-insect systems. But this quibbling is a little unfair, especially since the authors shun simplistic or dogmatic answers and themselves point out the limitations of our understanding regarding insect herbivores.

Insects on Plants is a first step toward a community ecology for herbivorous insects. Although there is much to disagree with in the book (indeed I am sure the authors intended it that way), it should be widely read. Entomologists could profit by using the book to extend their typical emphasis on autecology. Meanwhile, ecologists (especially American community ecologists) would do well to adopt some of Strong, Lawton, and Southwood's population-level orientation toward testing and developing community theory. It might even turn out that the taxon-prescribed approach represented by *Insects on Plants* is a way of escaping the divisive and ill-posed debates now plaguing community ecology.

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Neo-Darwinism in Disfavor

Beyond Neo-Darwinism. An Introduction to the New Evolutionary Paradigm. MAE-WAN HO and PETER T. SAUNDERS, Eds. Academic Press, Orlando, Fla., 1984. xiv, 376 pp., illus. $40.

Neo-Darwinism began with Weissman's rejection of Lamarckian inheritance and matured in the "modern synthesis," from the 1930's to the early 1950's. A simplistic, false, but remarkably widespread view of this synthetic theory is that it was a simple union of Darwin's theory of natural selection with the mechanistic theory of Mendelian genetics. In this conception, neo-Darwinism is equated with "natural selection of random variations," as the editors of this volume phrase it. Much of the current, less incisive evolutionary literature might indeed lead one to this equation, for the "adaptationist program," under which all traits are adaptive and nearly ideally so, has a firm grip in some quarters. But both the Panglossian adaptationists and the critics of neo-Darwinism fail to appreciate the richness, the plurality, of evolutionary mechanisms inherent in the synthetic theory.

To be sure, natural selection and random mutations were a dominant focus of the modern synthesis. The synthesis came about, after all, largely as a reaction against various neo-Lamarckian,

mutationist, and orthogenetic theories that were bruited about at a time when natural selection had fallen almost entirely into disrepute. But the synthesizers arrived at a complex body of evolutionary mechanisms. Wright, who influenced Dobzhansky and through him the rest of the company, included genetic drift and interdemic selection in his theory. Simpson sought both to reconcile paleontological patterns with genetics and to explain patterns of diversification and extinction. Mutation was held to be random: not that all variations are equally likely, but that mutations are not biased toward adaptedness. Development, it was clear, constrains the variety of mutant phenotypes, and developmental explanations were offered for phenomena such as parallel evolution. Wright, Dobzhansky, Mayr, and Stebbins emphasized pleiotropy and firmly rejected an atomistic view of development and morphology. And if the neo-Darwinians rejected the inheritance of acquired characteristics and emphasized mutations of small effect over saltations and nuclear genes over cytoplasmic inheritance, they did so on the basis of empirical evidence, not the demands of theory.

No one will argue that neo-Darwinian theory has addressed all evolutionary questions exhaustively or that it cannot be modified by new information on the mechanisms of heredity and development. But it is one thing to call neo-Darwinism incomplete; it is quite another to call it fundamentally wrong. The latter, however, is the view of many of the authors in this book. Their common theme (notwithstanding the editors' denial) is dissatisfaction with the neo-Darwinian framework. Politics has seldom made stranger bedfellows than are found between these covers.

Some of the authors share a preference for holism over reductionism. This presumably explains the inclusion of chapters on artificial intelligence (Boden) and cognitive psychology (Sinha) and a curious chapter on self-organization by Matsuno ("Evolution of matter is a mode of matter constraining itself by itself, not an outcome selected by something else"; p. 85). Ignoring the literature on mutation and protein synthesis, Fox extrapolates from his origin-of-life experiments to the conclusion that protein sequences evolve orthogenetically, mutation being constrained by (undocumented) principles of self-organization. Wicken, in a generally unexceptionable argument for the thermodynamic possibility of increased complexity, carries holism to the ecosystem level: the adaptive strategies of individual organisms will generally "contribute to the higher ecosystem good—i.e., the power and complexity of ecosystem flow." This view has not been supported by any mechanistic models that I know of.

Vrba and Nelson and Platnick pursue quite different themes. Vrba takes little issue with neo-Darwinism except to lament that it has neglected the role of differential proliferation of groups of species in macroevolution. There is some truth in this charge, although theories of speciation and of species diversity certainly touch importantly on this issue. If Vrba's chapter is innocent, Nelson and Platnick's virulent attack on Darwinism is not. They make the extraordinary claim that Darwinism has been found false because it is impossible to fulfill part of the Darwinian program, tracing ancestor-descendant series of taxa. Paraphyletic groups (those which, like the class Reptilia, have had descendants, such as the Mammalia, excised) are not permissible in Hennig's system of classification. Ancestral taxa are by definition paraphyletic, so phylogenetic ancestor-descendant sequences must vanish. This is, transparently, verbal legerdemain.

The most interesting chapters are by developmental biologists. They rightly emphasize that organisms cannot be atomized into distinct parts, that epigenetic "rules" constrain the field of phenotypic variations, and that some developmental information resides in the egg's cytoplasm. Unfortunately, their arguments are flawed by their caricature of neo-Darwinism as a theory under which all variations are possible and by the utterly unwarranted dualism that Løvtrup, Goodwin, and Webster espouse. These authors reject genetics as the basis for similarities and differences among species. In their view, developmental programs are independent of, and transcendent to, DNA-based information—as if developmental fields or the organization of the egg were immune to alteration by mutation of DNA. And to provide physicochemical models of developmental events is not to replace genes and selection with a sufficient physicalist theory, as Goodwin believes; obviously the constituents of organisms obey physical laws, but these laws permit innumerable developmental patterns, of which only some are permissible under natural selection.

Happily, these dualisms do not as greatly mar the chapters by Saunders, Ho, and Pollard. Ho's description of the role of the cytoplasm in genetic assimilation is interesting, but in his enthusiasm about cytoplasmic inheritance he forgets the evidence for nuclear inheritance of the majority of variations within and among species. Pollard's review of the fascinating evidence that genetic information may be transferred from somatic to germ cells raises possibilities that should not be dismissed, but, as Fitch (*Evolution* **36**, 1133–44 [1982]) has noted, the fundamentals of neo-Darwinism are not violated unless an environmentally altered phenotype can further its continuance by altering its own genetic basis.

So this book is a very mixed bag. No one can fault the editors for their desire, widely shared, to see developmental biology more thoroughly incorporated into evolutionary thought. But they seem to have succumbed to the temptation to revolution, viewing modern evolutionary theory as an oppressive regime to be toppled rather than joined. In doing so, they have gathered together with the dispossessed, the Luddites, and the visionaries in a venture that must be slightly embarrassing.

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Geology of Southern Africa

Mesozoic and Tertiary Geology of Southern Africa. R. V. DINGLE, W. G. SIESSER, and A. R. NEWTON. Balkema, Rotterdam, 1983. viii, 375 pp., illus. $39.50.

Until the Mesozoic, southern Africa was the hub of Gondwana. Its Paleozoic and Mesozoic basins provide compelling evidence for the former contiguity of the supercontinent. Paleozoic deposition was initially concentrated in a linear downwarp along the southern margin of the craton, but through time the main depocenter migrated slowly northward. This history of basin evolution culminated in the Triassic Cape Orogeny. Large-scale vertical movements, extension, and rifting heralded a new phase in the geological evolution of the subcontinent. The present configuration of southern Africa is the result of the breakup of Gondwana in the early to middle Mesozoic and the spreading of the continental lithosphere to form the southwestern Indian and southeastern Atlantic oceans.

In the last couple of decades research and exploration have resulted in a burgeoning of information on the Mesozoic basins and ocean floors about southern Africa. Dingle and his co-authors have set out to review these data systematically and exhaustively, and they intentionally refrain from detailed interpretation.