Book Reviews

Population Interactions and Change in Biotic Communities

Stability and Complexity in Model Ecosystems. ROBERT M. MAY. Princeton University Press, Princeton, N.J., 1973. x, 236 pp., illus. Cloth, $11.50; paper, $4.95. Monographs in Population Biology, 6.

A 1969 Brookhaven symposium attended by many major population and community ecologists attempted to elucidate the relationship between diversity and stability in ecological systems. Success was so limited that the published proceedings led *Science*'s reviewer to conclude that the whole field might be stagnating and that what further progress would be made was perhaps to be sought in viewing each taxon and geographic region as idiosyncratic, forswearing a search for generalizations. Fortunately, the author of *Stability and Complexity in Model Ecosystems*, a physicist by training, has not heeded this admonition. He has undertaken to examine Levins's community-level analog of the Lotka-Volterra two-species predation and competition models, increase its realism through the incorporation of such factors as time delays and random environmental fluctuations, and test the resulting "community matrices" of species-interaction coefficients for mathematical stability of the underlying equations at several levels.

Neutral stability of a system simply implies that displacement of an equilibrium system ("equilibrium" meaning that population sizes are either constant or undergoing fixed oscillations) produces another equilibrium system, the parameters of which are determined only by the degree and direction of the displacement. Continuing cycles caused by neutral stability (like those produced by the Lotka-Volterra predation model) are dismissed as unrelated to cycles observed in nature, since once the amplitudes are set by environmental disturbance they remain constant indefinitely, no matter what environmental conditions prevail. Another major disturbance may reset them at some other levels, where they remain even if the environment after the last disturbance is the same as that preceding it. Limit cycles or points with neighborhood stability are equilibrium states such that a limited disturbance will be followed by return to the same amplitudes or positions, respectively. The author demonstrates that sophistication of the basic community matrix model frequently leads to stable limit cycles; for example, predator-prey systems are likely to exhibit stable limit cycles when the environmental carrying capacity of the prey is large and their intrinsic rate of increase exceeds that of the predators. The Hudson Bay lynx-hare system and other well-known natural population size cycles are related to stable limit cycles. Finally, structural stability is even more germane to robust biological models, for it implies that gradual changes in the underlying equations produce continuous, gradual changes in the equilibrium state (be it limit cycle or static point) and thus that the model itself can be modified without invalidating its results. Structural stability is treated only lightly, but the interesting point is made that one-trophic-level competition produces a structurally stable community matrix model, whereas predator-prey community matrix models are structurally unstable.

With neighborhood stability, then, as the main criterion, the author's chief conclusion is that, contrary to ecology's central dogma, increased species number and complexity of food web structure usually lead to *decreased* stability. Hence ecologists ought to focus on those particular types of complexity which produce mathematical stability, since there seems to be a high, but not perfect, correlation in nature between complexity of trophic structure and stability of the community, as manifested by continued existence of all its populations within limited size ranges. Stability of only one trophic level, viewed as a subcommunity with its own matrix, is shown usually to enhance stability of the whole community; but only in special circumstances does predation impart mathematical stability to an otherwise unstable group of competitors. The heralded work of Paine in the rocky intertidal and Janzen in tropical forests showing that richness of prey species is increased by predation thus corresponds to a very small subset of all possible mathematical models and parameters of predation. Mutualistic interactions are shown to be inherently destabilizing in a mathematical sense, and this may be the reason for their relative rarity in nature. Competitive interactions are likewise destabilizing (if the environment is at all variable), so one might have expected the inference that competition might be less important in complex communities than we have been led to believe. But competition is not claimed to be rare. Rather, it is an implicit article of faith in this work that competition must always be occurring, and that if a resource is relatively untapped the community or its component populations will quickly evolve to increase its utilization. Hard evidence on this point is scarce. Shifts in ecological niches ("ecological release") upon removal of putative competitors would be convincing, but MacArthur and Wilson pointed out six years ago that sometimes ecological release is clear and occurs quickly but that some species seem unable to modify their resource utilization patterns if new resources become available through the absence of former "competitors." There are depauperate island communities with apparently severe "underutilization" of resources. Subsequent research on both vertebrates and invertebrates has perhaps more often demonstrated subtle day-to-day competition than its absence, but several other instances of continuing resource underutilization have surfaced. Perhaps the biologically interesting community matrices will be large ones with many entries (interaction coefficients) of zero.

The incorporation of time delays in population interactions destabilizes a system, but if the time delays are small compared to the time scales of birth rates of the interacting populations, destabilization may only be from static equilibrium population sizes to stable limit cycles. An ecumenical result concerns the relative sizes of the vegetation recovery-rate time scale (T), the herbivore birth-rate time scale (T_1), and the geometric mean of T_1 and the carnivore birth-rate time scale (T_2). If T is between T_1 and T_2, the vegetation-herbivore interaction alone will be unstable, while addition of a carnivore will yield stability. The Isle Royale vegetation-moose-wolf data are aptly mentioned in this context, and it is pointed out that the controversy between Slobodkin, Smith, Hairston, *et al.* and Ehrlich and Birch on whether nature is balanced and what determines herbivore population size may be resolved: the number of herbivore individuals may well be set by predation, and may be much lower than that sustainable by the available vegetation, but the resource limitation term N/K in the herbivore population equation is necessary for stability of the system.

Randomly fluctuating environments simply yield equilibrium probability distributions instead of population sizes or cycles: "In the deterministic environment, we require only that the terrain slope upward from a stable equilibrium valley. In the stochastic environment, the landscape is heaving up and down like the floor of a fun-house." Both stability and mean population sizes are lower, but so long as the smallest community matrix eigenvalue is greater than the environmental variance, the random-fluctuation model does not produce strikingly new predictions. Unfortunately the analog of seasonality—periodically varying parameters—is not treated, and we are left only with the statement that there is a large mathematical literature on such models. Since this is perhaps the most biologically relevant of environmental fluctuation patterns, and Stewart and Levin have recently provided a theoretical demonstration that seasonal availability of resources can allow two competitors to coexist, I regret that this literature is unexplored.

The final major discussion is of limiting similarity of coexisting species and permissible overlap of their ecological niches. May builds on MacArthur's last competition work to show that if fluctuations in resource availability are small, overlap may be about as large as the width of the species' resource utilization functions (ecological niches), while if environmental fluctuations are severe or the niches involve several different resource sets (such as food or nest space) which are not independent, the permissible overlap is less and is determined by the environmental variance. These results hold even if resource utilization functions or availability curves are changed and accord well with available data, especially for vertebrates.

May aims his text at laboratory and field ecologists, with excellent graphs for biologists and appendices for mathematical esthetes. Despite his obvious effort to bring the mathematics within our grasp, much of the text is more formal than most ecologists will feel comfortable with, and my guess is that many in his target audience will read only the summaries. This is unfortunate, since the body of the book is clearly understandable if the effort is given and contains much unsummarized information. Particularly valuable is the demonstration that the plethora of mathematical models oppressing today's ecologists are variations on just a few simply stated themes. One point that begs for more frequent reiteration for biologists is that mathematical neighborhood stability may exist with negative values (extinction) for some component populations. In one such case, *any* matrix of competitors (all matrix entries being positive) represents a mathematically stable system, but that does not mean that the competitors can all coexist. Another consequence of this mathematical treatment is that for a group of competitors in a deterministic environment an increase in species number does not decrease mathematical stability; but if there is *any* random environmental variation the new systems will be less stable. Similarly, mathematical stability sets no limit to niche overlap if the environment is static; in fact in larger, more tightly packed communities the squared deviation of resource availability from resource utilization, which is what MacArthur claims is minimized by competition, is lower. But again, environmental variability will limit the packing compatible with continued existence of all competitors, so that permissible overlap is at best equal to the width of the resource utilization functions (niche width). All of this is stated in one way or another by May, but the nonequivalence of mathematical neighborhood stability and biological coexistence should have been made more explicit. An evaluation of Levins's and Vandermeer's work on the number of permissible extant populations in a community with matrix entries having certain properties would have been in order.

The author is explicit about the assumptions and limitations of his models, and deliberately omits two phenomena that bear importantly on community stability. The effects of spatial heterogeneity are, of course, a subject of active inquiry, and notable work by Chitty, Wellington, Pimentel, and others indicates that genetic change (evolution) may occur over very few generations to modify the population parameters in the ecological models, possibly effecting a homeostatic maintenance of one or more interacting species. Genetics may also provide the explanation of why ecological release occurs in some instances and not in others. Given the assumptions, the predictions from the community matrix approach are assiduously compared to available data (the bibliography is exhaustive in both mathematics and biology) and conform quite well. But one is left with the disquieting feeling, perhaps inevitable with moderately complex general models, that models based on conflicting assumptions might also have generated these predictions, and it is disturbing that the data are usually tested against rather tortuously achieved results. Biological information is available for comparison to much more basic aspects of the community matrix method and does not completely dispel the unease. For example, the entire elegant edifice is currently constructed on the assumption that higher-order interactions (for example, two species' having an interaction that is detrimental to a third species) are unimportant and can be neglected in manipulating equations. Higher-order interactions were unimportant in Vandermeer's artificial community of four competing ciliates, but Hairston *et al.*'s three-trophic-level, eight-species experimental communities of bacteria and protozoans and Wilbur's experimental community of three salamanders produced just the opposite indication.

This volume treats so many topical problems and proposes so many hypotheses that one might expect it to stimulate considerable field and experimental work on topics such as those discussed above, as its predecessors in the Princeton monograph series have done. Merely as an exhaustive synthetic review of much of the population and community model literature it would be a standard reference for graduate workers in the field. In addition, as a clear, elegant, and provocative treatise in an area of theoretical and practical importance, it unites with MacArthur's *Geographical Ecology* to reverse the trend to senescence in diversity-complexity-stability studies and to motivate new research on a variety of levels.

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