BOOK REVIEW: AN INTRODUCTION TO MATHEMATICAL ECOLOGY

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Abstract

A review of, and reader's aid for, the text by E. C. Pielou.

Mimeo series, Biometrics Unit, Cornell University.

PIELOU, E. C. An Introduction to Mathematical Ecology. Wiley-Interscience, New York, 1969. viii + 286 pp., $14.95.

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To be most fair to this book, one should perhaps evaluate it on the basis of what it does rather than on whether it does what it claims. The book has some real strengths, some glaring weaknesses. On balance, it will perform a real function for many who have had to go to myriad references in the past, many of which are more mysterious than this one, to discover the things now contained in one source. However, it fails on several counts, and we shall list these first.

Pielou's An Introduction to Mathematical Ecology is not properly that. It totally ignores too much of mathematical ecology for it to perform the function implied by the title. Furthermore, although the problems discussed are ecological in origin, the clear emphasis of the book is on the mathematics. Insufficient discussion is given to both the realism of the assumptions underlying the mathematics and the possible ecological implications of the results. The treatment of population dynamics ignores the bulk of the extensive current literature on that topic. No attempt is made, for example, to find relationships between such topics as the dynamics of community interactions, the structure of the trophic web, community energetics, species-abundance relations and community stability theory. Thus Pielou treats all but the first of these topics at best as static ideas and misses the real insights available. Similarly ignored is the work of those concerned with the management of resources and populations. The book, in spite of these omissions, is useful. It is simply misnamed.

In addition, despite its stated objective of being a text for ecologists, the book requires of the reader a mathematical background which few ecologists are likely to possess. It seems far more suitable for students in biometry and statistics seeking applications of their training. For even a cursory reading, one must be comfortable with the basics of the calculus, of differential equations, of matrix algebra and of probability and statistics. In order to read it in depth, one needs to have a working knowledge of such topics as probability density functions, probability generating functions, Markov processes and the theory of estimation and hypothesis testing. Moreover, those who, unable to follow the derivations from assumptions to results, simply attempt to implement those results, run a risk of using inappropriate techniques, since many of the procedures are by Pielou's own admission based on hypotheses which are, at best, of dubious reality.

Before restricting attention to selected specific details, some general comments are in order. The quality of the mathematics has a reasonable mean but a very high variance. There are some clever mathematical analyses, some of which are relevant to biology. There are other places where the mathematics is cumbersome. Despite her promise to the contrary, there are too many places where the author has leaned heavily on tecnhiques equivalent to "the mathematician's daunting phrases 'obviously therefore . . .' and 'clearly then . . .'". Furthermore, the mathematically inclined reader will likely bristle at the lack of definitions. For example, in the first two paragraphs of page 27, the words "quasi-stationary", "ultimate stationary", "equilibrium", and "statistical equilibrium" are used, all without formal definitions. Such definitions would have done much to improve readability. Finally, and most inexcusably, there are a few places where the mathematics, and worse still the results, are simply incorrect. But we shall be more specific in the detailed analysis.

On the positive side, there are several topics (e.g., principal components analysis, contingency tables) for which the author points up potential problems in the standard methods of analysis. There are other areas where she has presented a reasonable survey of what current technique is, even when the state of the art is not on firm footing.

The following detailed analysis is to serve as an aid to the reader of the text, and is meant to be used in conjunction with the text.

I. Population dynamics: As noted previously, the main weakness of this section is its lack of depth and breadth. The theory of population biology is not what it was ten or fifteen years ago; yet the changes have not been noted in this book. Only a handful of papers since 1960 are even mentioned. The discussion of the classical literature is adequate. Unfortunately, the book does not go far enough.

On p. 13, Pielou gives the value i/μ as the expected time to extinction of a population of initial size i undergoing a pure death process with constant death rate μ per individual. The correct answer is $\frac{1}{\mu} \sum_{j=1}^{i} \frac{1}{j}$. To see this, suppose that $\{N(t);\ t \geq 0\}$ is a pure death process with parameters $\mu > 0$ and $N(0) = i$, so that $P[N(t) = k] = \binom{i}{k}\left(e^{-\mu t}\right)^k\left(1-e^{-\mu t}\right)^{i-k}$ for $k=0,1,2,\cdots,i$. Then if τ_j is the time to first death in a population of initial size j, its distribution function is $P[\tau_j \leq t] = 1 - P[N(t) = j] = 1 - e^{-\mu t j}$, and it has mean $E\tau_j = 1/(j\mu)$. Now the time to extinction of a population of initial size i is the sum of times between successive deaths, i.e., $\tau_i + \tau_{i-1} + \cdots + \tau_1$. Thus the expected time to extinction is $E\Sigma_1^i \tau_j = (1/\mu)\Sigma_1^i (1/j)$ as stated. Pielou's reference to the footnote on p. 120 as justification for her formula is not appropriate since that footnote refers to a different process, namely one in which the mean number of deaths per unit of time is μ, independent of the population size. For the pure death process on p. 12, the mean number of deaths per unit of time is $j\mu$ for a population of size j.

On p. 36, the notion of a "long-continued process" is not relevant to the discussion and should simply be deleted.

Several potentially confusing points occur in the discussion of the stable age distribution on pp. 36-37. There is a serious problem concerning the existence and uniqueness of a stable age vector; that is an eigenvector (of a certain matrix) with no negative elements and with a corresponding positive eigenvalue. There is an associated mathematical theory, the Perron-Frobenius theory (see for example Varga, 1962, Matrix Iterative Analysis, Prentice-Hall) which deals with this question. Pielou need not deal with the theory, but some indication of the nature of the problem would be elucidating and justify her reference to "the stable vector". A further point of clarification is in order concerning the fact that "the stable vector" is not unique, since any multiple of that stable vector is again stable.

On p. 43, reference is made to the situation "described by the equation $N_t = N_o e^{rt}$, or, alternatively, $N_{t+1} = N_t e^r$," where N_t is the population size at time $t \geq 0$, and r is a constant. It should be pointed out that these two situations are neither equivalent nor true alternatives, and it is the first that Pielou really discusses. If $N_t = N_o e^{rt}$ for all $t \geq 0$, then clearly $N_{t+1} = N_t e^r$ for all $t \geq 0$, but the reverse is simply not true.

Formula (4.6), p. 47 is not complete, since it is missing the limits of integration. It should be $R_o = \exp\left(\int_o^r A(\hat{r})d\hat{r}\right)$. A typographical error appears on p. 51 where the formula should read $T_x = \sum_{j=x}^{w} L_j$.

II. Spatial patterns in one-species populations: On p. 115, it is incorrectly asserted that a certain statistic A has expected value 1. In fact $A = x/(1-x)$ where x has the beta distribution with probability density function $g(x) = [B(n,n)]^{-1}x^{n-1}(1-x)^{n-1}$ for $0 < x < 1$, $n > 1$. Thus $EA = n/(n-1)$.

On p. 117, in two places $\frac{1}{2}\sqrt{\rho}$ should read $\frac{1}{2}/\sqrt{\rho}$. On p. 118 in three places, the estimated α should be written as $\hat{\alpha}$. On p. 120, the variance of ω_n is n/λ^2, not n^2/λ^2.

The discussion of the diagram on p. 120 is not strictly correct. For example, there are points in the right half of the rectangle which are nearer to A than to C.

III. Spatial relations of two or more species: It is asserted on p. 186 that for a certain random variable, L, $E(1/L) = 1$. In fact, this is only an asymptotic result, as is made clear in the reference cited.

IV. Many-species populations: It appears that the α's in the display on p. 211 should all be γ's.

The discussion on p. 257 is not technically correct. It is indeed possible to make a one-to-one identification between the non-zero latent roots of R and Q, and between their corresponding latent vectors. This is not shown on p. 257, but the demonstration which is made presupposes it. Moreover, it is not correct that such an identification can be made for the latent vectors corresponding to zero latent root, since there are not the same number of such vectors which are linearly independent.

On pp. 258-260, there are several confusing points. First, what is an "acceptable" definition for m_{ij}? Presumably, this measure of "difference" must be a metric, so that for example $m_{12} + m_{23} \geq m_{13}$. Second, no motivation is given for why one should be interested in the "distance" measure sought. Third, contrary to the author's claim, a "distance" is derived which is only proportional to the "difference" measure m, not equal. Although this is a small point, the assertion of the text is misleading. Finally, in the discussion of the latent roots of A, beginning with the determinantal equation $|A-\lambda I| = 0$, Pielou has replaced the matrix "A" by the matrix "$\frac{3}{4}A$". Thus the latent roots determined are those of "$\frac{3}{4}A$", not of A itself. Despite her disclaimer, "Neglecting the factor $\frac{4}{3}$,..." the notational change is very confusing.

Formula (21.1) is wrong. The population covariance matrix Σ is not $\begin{pmatrix} X \\ Y \end{pmatrix}(X'Y')$.