

SOME CRITICAL CONSIDERATIONS OF THE THEORY OF SPECIES PACKING

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ABSTRACT: A critical consideration of both the deterministic and stochastic models of species packing is presented. The assumptions, both implicit and explicit, of each of the models are examined in detail and the importance of these assumptions to the predictions of the models is discussed. From these analyses it appears that: (1) the present models of species packing are so weakened by their many unrealistic assumptions that they are unable to provide an adequate description of species interactions in natural communities; and (2) further speculation within the framework of the present models is unlikely to be productive.

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INTRODUCTION

In recent years there has been a great deal of interest generated by the questions of how species are arranged along resource gradients and to what extent niche overlap among species may be governed by some sort of ecological laws. Data gathered on bird species and first remarked on by Hutchinson (1959) seem to have sparked the theoretical considerations of species packing, which at present have greatly outstripped the evidence needed to test them. The papers of MacArthur and Levins (1964, 1967) served to usher in the development of this new era of ecological interest in an old problem. The theory of species packing has diverged since these original papers, with May (1973, 1974) and May and MacArthur (1972) developing a model allowing for stochastic fluctuations in the resource spectrum while others (Levins 1968; Rescigno 1968; Vandermeer 1970, 1972; Culyer 1974; Cody 1974; Hespenheide 1973; Roughgarden 1974) have chosen to follow the original deterministic approach of MacArthur and Levins.

At this stage in the development of the theory of species packing it seems appropriate to evaluate the two approaches and to examine the assumptions, both explicit and implicit, which underlie each of these models. This is necessary, since there is a danger that untested models may become incorporated into ecological "axioms" which are accepted as being true only because "theory tells us" that they should be true. Indeed, this danger has been made more apparent by the comments of several anonymous reviewers of this manuscript. For example, one of them points out that the theory of species packing is the only "rigorous" explanation which purports to account for a number of patterns observed in natural communities. Hence, he feels that the theory will not be given up until a new one is proposed to take its place - even if the current theory is wrong or irrelevant. Therefore, since I do not propose a new synthetic theory of species packing herein, he recommended that the manuscript not be published. Yet anyone familiar with the

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workings of science will recognize the weakness of this criticism. Progress can be made solely from the criticism of currently accepted theories, independent of the proposal of new hypotheses (Popper 1965).

In this paper I provide a critical review of the esoteric theory of species packing, and expose in some detail its many debilitating implicit assumptions, for those who may not have previously considered this body of theory in depth. It then becomes an individual decision whether to continue to order one's thoughts within this framework, once its intricacies have been openly evaluated, or to forsake this line of reasoning, even though the alternative is the lack of a synthetic theory of species packing.

THE MODELS OUTLINED Deterministic Model

This is the original model of species packing developed by MacArthur and Levins (1964, 1967) and it has been termed "deterministic" by May (1973) because it assumes that all environmental parameters are strictly constant. The following development of the model is taken from MacArthur and Levins (1967).

The model assumes that a community of n species obeys the Lotka-Volterra equations: (1) $\frac{dX_i}{dt} = r_i X_i (K_i - X_i - \sum_{j=1}^n a_{ij} X_j)$, where X_i is the

abundance of the i^{th} species; r_i is the intrinsic rate of increase of the i^{th} species; K_i is the carrying capacity of the i^{th} species; and a_{ij} is the effect of species j on species i , measured in units of species i . The community will retain all of the n species if any particular one of them can increase while it is rare and all others are at their equilibrium values; that is, if $K_i > \sum_{j=1}^n a_{ij} X_j^*$ for all i , where X_j^* are the equilibrium values which satisfy $K_j = X_j + \sum_{k=1}^n a_{jk} X_k^*$.

Now, if three species are competing on a one dimensional resource gradient, and the middle one (X_2) competes heavily (signified by α) with the two outer species and both outer species compete only weakly (signified by β), we have the conditions specified by the MacArthur and Levins model. It is also assumed that $K_1 = K_3 = K$ and $\alpha_{12} = \alpha_{32} = \alpha'$. The equations for three such species can be written-following (1)-as:

$$(2a) \frac{dX_1}{dt} = r_1 X_1 \frac{(K - X_1 - \alpha' X_2 - \beta X_3)}{K}; \quad (2b) \frac{dX_2}{dt} = r_2 X_2 \frac{(K_2 - X_2 - \alpha X_1 - \alpha X_3)}{K};$$

$$(2c) \frac{dX_3}{dt} = r_3 X_3 \frac{(K - X_3 - \beta X_1 - \alpha' X_2)}{K}.$$

Since the middle species is under the most intense pressure, the three species will persist only if $K_2 > \alpha X_1 + \alpha X_3$. From (1) when only two species compete then the conditions for coexistence become:

$$(3a) \frac{K_2}{K} > \frac{2\alpha}{1+\beta}; \quad \text{conversely, species two cannot coexist when } (3b) \frac{K_2}{K} < \frac{2\alpha}{1+\beta}$$

Visualizing, with MacArthur and Levins, the competition coefficients as overlaps in resource utilization between species, one can construct a graphical model and a method for computing competition coefficients. The

$U_i(R)$ of Figure 1 represent the amount of resources utilized by a species i . Then the competition coefficients for, say species 1 and 2, are proposed to be represented in the case where resources are renewed constantly as

$$\alpha = \frac{\int U_1(R)U_2(R)dR}{\int (U_1(R))^2 dR} \quad \text{for continuous resources and by } \alpha = \frac{\sum U_1(R_i)U_2(R_i)}{\sum (U_1(R_i))^2}$$

in the case of discrete resources. (Where α represents the probability of the simultaneous presence of individuals of two species relative to the probability of the presence of two individuals of a single species.)

If the resource utilization functions describe normal curves, as in Figure 1, and these curves have equal variance, which is equivalent to having equal niche breadth (signified by H), and differ in location only by an amount D , then $U_1(R) = e^{-\frac{X^2}{H^2}}$, $U_2(R) = e^{-\frac{(X-D)^2}{H^2}}$, and $U_3(R) = e^{-\frac{(X-2D)^2}{H^2}}$.

Therefore, $\alpha = \frac{\int \exp(-X^2/H^2 - ((X-D)^2/H^2)) dX}{\int \exp(-X^2/H^2)^2 dX} = \frac{-D^2}{e^{2H^2}}$. In the same manner,

$\beta = e^{-\frac{2D^2}{H^2}} = \alpha^4$. Then additionally assuming that $K_2 = K = K_1 = K_3$, we have

from (3b) upon substituting $\alpha^4 = \beta$: $1 = \frac{2\alpha}{1+\alpha}^4$, which simplifies to $\alpha = .544$.

Thus, given all the above assumptions, species 2 cannot invade for $\alpha > .544$.

This corresponds to a separation, D , between U curves of 1.1 H units

(by solving $e^{-\frac{2D^2}{H^2}} = .544^4$). Therefore, if the resources are distributed

uniformly, the total number of species which can survive in a one dimensional array of resources is approximately the quotient of the environmental range and the niche breadth (H).

By allowing K 's to vary and assuming α and β are those for normal shaped U curves, MacArthur and Levins deduce relationships predicting the likelihood of invasion for different ratios of K_2 ($= K$ invader) and K ($= K_1 = K_3 = K$ resident) (see their fig. 2). They summarize their model by noting that "species packing can be close if the K 's are uniform, if the niche dimension is high, or if the niche breadth, H , is small." MacArthur and Levins also note that if the area of competition involves more than one dimension the above results no longer hold, and, in general, n species can coexist in an $n-1$ dimensional niche space which is subdivided among competitors.

Roughgarden (1974) has extended the MacArthur and Levins model by considering a whole family of different shaped utilization curves and corresponding "competition functions." This work is based on the same assumptions as the original model but generates new predictions. Invasion of a species will be most likely if (1) the invader has a carrying capacity larger than that of the average carrying capacity of the residents, (2) the resource utilization curves are platykurtic for a constant variance of utilization over the resources, and (3) there is an "invasion barrier" to successful colonization which covers a range of values between residents and invader. Invasion may occur for values below and above the "invasion barrier." It should be emphasized that these conclusions pertain only to a one-dimensional array of resources.

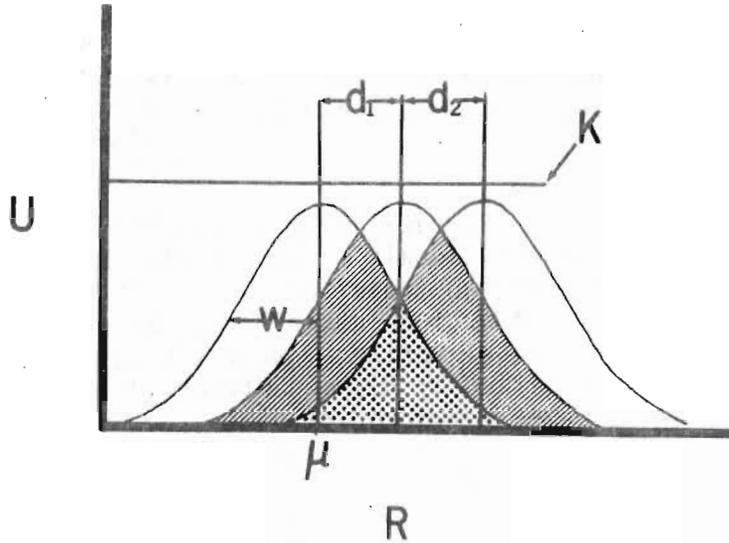


Fig. 1. U is the probability of utilization of resource R in a unit time by an individual. The curve K represents a resource continuum that sustains various species whose utilization functions are distributed normally with mean μ and standard deviation w . The area under each curve is the total resource utilization, K_i , for species i . The stippled area = β , the hatched area = α and $D = d_1 = d_2$ in the MacArthur and Levins (1967) deterministic model.

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Hespenhide (1973), working with the same model, has investigated the case where variances of resource utilization curves are not equal. He has used prey size utilization curves for different species of birds to compute competition coefficients, where $\alpha_{ij} = \sum p_i p_j / p_i^2$ represents the competitive effect of species j on species i , and $\alpha_{ji} = \sum p_i p_j / p_j^2$ represents the competitive effect of species i on species j (where $p_i = U_1(R_i)$ and $p_j = U_2(R_j)$ in the MacArthur-Levins notation). It can be seen that the species which has the smaller variance in its resource utilization curve must have a greater competitive effect than the other species since $\sum p_i p_j$ is constant. Predictions arising from this treatment show that if the ratio of the variance of the larger to the variance of the smaller curve is less than about 1.5 there is little change in the α values which are predicted when the variances of resource utilization curves are assumed equal. However, ratios greater than 1.5 cause relatively large changes in α 's predicted under the assumption of homogeneity of variances (i.e., under the assumptions of the original MacArthur-Levins deterministic model).

Thus, by relaxing or changing some of the assumptions of the original deterministic model quite different predictions about species packing may be generated. The significance of this will be considered later in this paper.

Stochastic Model

The so-called stochastic model (May 1973) has as its springboard the equation (4) $\frac{dN_i(t)}{dt} = N_i(t)(k_i - \sum a_{ij} N_j(t))$ $a_{ij} \geq 0$; $k_i > 0$, where k_i are

integrals with respect to X over the product of the resource spectrum and the utilization function of the i th species, and the competition coefficients a_{ij} are convolution integrals between the utilization function of the i th and j th species (May and MacArthur 1972). This equation was originally developed by MacArthur (1969, 1970) and ensures that total community utilization of the resource spectrum will provide the best least squares fit to the total resource spectrum. In order to understand better the stochastic model and its assumptions, I will first trace the origin of equation (4).

Assume, after MacArthur (1969, 1970, 1971), that X_i is the abundance of species i , which grows according to the equation (5) $\frac{dX_i}{dt} =$

$c_i X_i (\sum a_{ij} w_j R_j - T_i)$ where c_i is a constant of proportionality governing conversion of grams of resource R into grams of X_i ; R_j is the abundance of resource j ; w_j is its weight in grams; a_{ij} is the probability that an individual of species i encounters an individual of species j ; and T_i is a threshold quantity of available food below which X_i decreases. Also assume that the resource population grows according to (6) $\frac{dR_j}{dt} = r_j R_j (K_j - R_j) - \sum a_{kj} X_k R_k$, where r_j is the intrinsic

rate of increase for resource j ; K_j is the carrying capacity of the habitat for resource R_j ; and a_{kj} is similar to the a_{ij} in (5). These equations - (5) and (6) - are the Lotka-Volterra predator-prey equations with a self-limitation term added to the resource equation.

Rearranging equation (6), we have $\frac{dR_j}{dt} = \frac{r_j R_j}{K_j} (K_j - R_j - \sum \frac{K_j}{r_j} a_{kj} X_k)$.

At "equilibrium" $\frac{dR_j}{dt}$ is near 0, and the following can be considered to

be approximately true; (7) $R_j = K_j - \sum \frac{K_j}{r_j} a_{kj} X_k$. By substituting this

value of R_j in equation (5) it is found that:

$$(8) \quad \frac{dX_i}{dt} = c_i X_i \left(\sum a_{ij} w_j K_j - T_i - \sum \frac{a_{ij} w_j K_j}{r_j} X_k \right)$$

Then at "equilibrium" when both the X 's and R 's are constant:

$$(9) \quad a_{ij} w_j K_j - T_i - \sum \frac{a_{ij} w_j K_j}{r_j} X_k = 0.$$

Now the following assumptions are made: (1) All species have the same threshold requirements (i.e., $T_i = T$); (2) all species have the same total harvesting abilities, $\sum a_{ij} = a$, independent of i . Then the following can be formed: (10) $Q = \sum \frac{w_j K_j}{r_j} \left(r_j - \frac{T}{a w_j K_j} \right) - \sum a_{ej} X_e)^2$.

This expression is a weighted (by wK/r) squared deviation of "available

production" $(r_j - \frac{Tr_j}{aw_j K_j})$ from the species harvesting abilities $(\sum a_{ej} X_e)$.

The partial derivative of equation (10) is

$$(11) \frac{\partial Q}{\partial X_i} = -2(\sum a_{ij} w_j K_j - T - \sum a_{ij} a_{kj} w_j K_j X_k) \frac{r_j}{r_j} X_i$$

$$(8) \text{ and substituting, we have (12) } \frac{dX_i}{dt} = -\frac{1}{2} c_i X_i \frac{\partial Q}{\partial X_i}$$

the derivative of Q with respect to t, we find that

$$(13) \frac{dQ}{dt} = \sum \frac{\partial Q}{\partial X_i} \frac{dX_i}{dt} = -\frac{1}{2} \sum c_i X_i \left(\frac{\partial Q}{\partial X_i}\right)^2 < 0$$

Therefore we have established Q as a minimum at the "equilibrium" points $\frac{dR_j}{dt} = 0$ and $\frac{dX_i}{dt} = 0$, and have

shown that equations (5) and (6) lead to the criterion that the total resource utilization of a group of competing species will provide the best least squares fit to the total resource spectrum.

Now to get back to the form of May's (1973) equation (4), let the terms in brackets in equation (8) equal K_i and a_{ij} respectively.

$$\text{Equation (8) can then be rewritten as (13) } \frac{1}{X_i} \frac{dX_i}{dt} = c_i (K_i - \sum a_{ij} X_j)$$

by replacing X_i by $c_i N_i$ and $a_{ij}/c_i c_j$ we have the "canonical form" as in equation (4). I now return to the further development of the stochastic model.

If it is assumed that the resource utilization functions of the competing species represented by equation (4) are Gaussian curves, each of a common width, w , and that they are uniformly spaced along the resource continuum (i.e., $d_1 = d_2$ in Figure 1), the competition functions can be written as (14) $a_{ij} = (w^2 \pi)^{-\frac{1}{2}} \int_{-\infty}^{\infty} \exp \left(\frac{-X^2 - (X - (i-j)d)^2}{2w^2} \right)$. By

substituting $a = \exp(-d^2/4w^2)$, (14) can be written as

$$(15) a_{ij} = (a)^{(i-j)^2}$$

Then, if we assume that all species in the equilibrium community have the same population size, the competition matrix (May and MacArthur 1972) can be written as:

$$A = \begin{bmatrix} 1 & a & a^4 & a^9 & \dots & a^{n^2} \\ a & 1 & & & & \\ a^4 & & 1 & & & \\ a^9 & & & 1 & & \\ \vdots & & & & \ddots & \\ a^{n^2} & & & & & 1 \end{bmatrix}$$

We can now deduce the stability of this symmetric (since we assume that $a_{ij} = a_{ji}$) matrix of competition coefficients by considering its smallest eigenvalue (May and MacArthur 1972). May and MacArthur then show that in a strictly deterministic environment, given the above assumptions, stability sets no limit to the amount of species packing; in fact, the more species that are packed in the better the least squares fit to the resource spectrum.

If, however, there is random variation in environmental factors, the k_i in equation (4) will not be constant. They can be assumed to be of the form $\bar{k}_i = \bar{k}_i + \delta_i(t)$ where \bar{k}_i is the mean of the k_i , and $\delta_i(t)$ is random "normal" variation with variance σ^2 . May and MacArthur then assume that species populations can be approximated by a multivariate normal distribution when the environment fluctuates and state that the probability of becoming extinct will be small if the smallest eigenvalue (λ) of the community matrix (the criterion for stability) is less than σ^2/\bar{k} . They then show graphically that if the environmental variation is less than about 30% of its mean value the conditions for stability require that the eigenvalues of the community matrix be greater than 0 by an amount which is approximately proportional to the width of the utilization functions. If the environmental fluctuations are greater than about 30% the species packing consistent with stability becomes proportional to the magnitude of the environmental variability.

The results predicted by the stochastic model may be summarized by observing that if consumer species populations grow according to equation (5) and their resource populations grow according to equation (6), and the additional assumptions made above hold, then in an unvarying environment there is no limit to the degree of niche overlap which is consistent with the mathematical stability of these interacting species populations. In a randomly varying environment in which the environmental variability is not large, species packing has a limiting value roughly equal to the width of the utilization functions; if the fluctuations in the environmental parameters are severe, then the species packing is roughly proportional to the environmental variance. It should be emphasized that these results pertain only to one dimensional competition, as did the previous deterministic model. In addition, the environmental fluctuations are assumed to affect only the resource populations and not the populations of the competing species themselves.

DISCUSSION

It is interesting to note that the deterministic and stochastic models predict quite different results for the case in which the environment is considered to be unvarying. The deterministic model predicts a limiting similarity among species (approximately equal to an α value of .544) while the stochastic model predicts no limit to the similarity among competing species in a strictly unvarying environment. There is evidence available for species kept in constant laboratory environments which suggests that closely related competing species cannot coexist (Gause 1934; references in Miller (1967)), thus supporting the deterministic model's conclusion that there is a limiting similarity among species. However, there is also evidence which shows that competing species in unvarying laboratory environments may coexist for long periods of time (references also in Miller (1967)), thus tending to support the conclusions of the stochastic model. In other words, either model may be supported by existing data; obviously both are not correct. We are then faced with two moderately complex models, both starting with the same initial framework (the Lotka-Volterra equations) but making different additional assumptions which have led to dissimilar conclusions. In fact, as mentioned previously, varying the assumptions within the deterministic model's framework has led Roughgarden and Hespenheide

to different conclusions than MacArthur and Levins. It is not hard to show that similar changes within the stochastic model's assumptions would lead to somewhat different predictions than the original ones of May and MacArthur. I now try to determine if one, or any of the above models seems to be applicable to species populations in the real world by examining some of the assumptions, both implicit and explicit, which are required for the predictions of them to hold. I have chosen those assumptions I consider to be most important in evaluating the applicability of the models. There are additional assumptions not considered here which may also be important; hence, this list should be considered a conservative one.

Deterministic Model

1. Assumptions of the Lotka-Volterra model of species interactions. Since the deterministic model is based on the Lotka-Volterra equations, it is necessary to summarize the assumptions required for them to hold.

- a. All individuals in a population are considered equivalent; i.e., there are no differences in fecundity, mortality, etc., among individuals of different age (Slobodkin 1953).
- b. The effect of one individual on another is independent of density (Smith 1952); i.e., at equilibrium α_{ij} are not a function of the X_i .
- c. Competing species have an additive effect on the capacity of a species to increase. This means that each individual removes a constant share of the resources which increases the term $(K_i - X_i)$ by an amount which is independent of the other in-

K_i

dividuals in the community. This assumption does not allow for any higher order interactions in which, for example, two species may have an interaction that is detrimental to a third species (Wilbur 1972).

These assumptions are likely never to be satisfied in nature and in the few cases where moderately complex species associations have been studied (e.g., Hairston et al. 1968; Neill 1974; Wilbur 1972), they have been found to be violated in such a way that the Lotka-Volterra equations could not adequately describe the outcome of competitive interactions.

2. Species compete on a one-dimensional resource continuum and that single resource for which they compete must be the only factor limiting the competing populations. This type of situation may hold for some species of birds (MacArthur 1972, and references therein), but it is to be expected that most other species of organisms which are not members of the highest trophic levels will not show such a relationship (May 1973; Schoener 1974b).

3. The formulae $\alpha = \frac{\sum U_1(R_i)U_2(R_i)}{\sum (U_1(R_i))^2}$ and $\alpha = \frac{\int U_1(R)U_2(R)dR}{\int (U_1(R))^2 dR}$

for discrete and continuous resources respectively, adequately measure the competition coefficients described by the Lotka-Volterra equations. In fact, these measures of α are untested models in themselves and, although reasonable, should not be accepted without testing their applicability (Schoener 1974a; Roughgarden 1974).

4. The resources for which species compete are instantaneously

renewed; i.e., there is no time-lag between utilization and reappearance of a resource. The approximate validity of this assumption is, of course, dependent on the type of resource being considered. However, in general, this assumption cannot be expected to be true.

5. The environment is unvarying. Therefore, no short-term fluctuations or seasonal changes can be accommodated by this model. In the real world environmental variation will certainly exist, and any conclusions drawn from this model would be suspect on the grounds of this assumption alone. This objection, of course, led to the development of the stochastic model.

6. The variance of the resource utilization curves are identical. Hespenheide (1973), as mentioned previously, has considered heteroscedastic utilization curves and has come to some conclusions which are different than those of MacArthur and Levins. I see no reason to expect that such curves would be homoscedastic in nature, and if they are not, then β (cf. page 3) is not directly transferable to a multiple of α . This is so because by MacArthur and Levins' definition of α , if the variance of one species utilization curve is less than another, the competitive effect of that species must be greater than that of the other. Hence, the result that α has a limiting similarity of .544 does not follow.

7. The resource utilization curves are congruent. Roughgarden (1974) has considered different sized curves of equal variance and has come to quite different conclusions than MacArthur and Levins, thus indicating that this assumption is important in obtaining their results. I see no reason to expect that this assumption would hold in nature.

Stochastic Model

The assumptions required for the development of the stochastic model will now be considered.

1, 2, 3, 4. Exactly the same assumptions and restrictions apply to this model as they did to the deterministic model, with reference to the Lotka-Volterra equations, one-dimensional competition, the untested measures of competitive effect, and instantaneously renewing resources.

5. The resource utilization functions are Gaussian curves. Although this probably is not so, May (1973) shows that any continuous function gives results which are not essentially different from that of normal resource utilization functions.

6. The variance (w) and the separation (d) of the utilization functions are constant. There seems to be no reason to expect this to be true, but May and MacArthur (1972) and May (1973) state that the results of the model are preserved if (w) changes in some systematic way along the resource continuum as long as the separation (d) changes similarly, thereby keeping d/w approximately constant. If (d) and (w) do not vary systematically, the results are not preserved. May (1973) cites some data referenced by MacArthur (1972, p. 65) as showing that d/w ratios among competing bird species do remain relatively constant, but my calculations do not support this. At the very least, the matter needs investigation.

7. The equilibrium populations of the competing species are considered to be equal. This is highly unlikely, although May (1973) claims that as long as all species are present in "significant numbers," the results of the model hold. It is not clear at present what "significant numbers" are.

8. a. The environmental variability, $\gamma_i(t)$, is normally distributed "white noise" (May and MacArthur 1972). May (1973) says this only requires that environmental fluctuations be correlated over short periods of time relative to other important time scales influencing the group of competing species.

b. The probability distribution of the competing species can be described approximately by a multivariate normal distribution. This assumption rests on 8a and "...applies when the (environmental) fluctuations are not too severe; that is, when the probability cloud is relatively compact" (May 1973). These random environmental fluctuations are assumed to cause similar fluctuations on the resources, thereby causing species populations to become multivariately normally distributed, since the i th population is expressed as the integral with respect to x over the product of the resource spectrum and the utilization function of the i th species (May 1973). As Darlington (1972) has pointed out, the environmental fluctuations are assumed only to indirectly affect population sizes through their effects on the resources. It might well be expected, however, that environmental fluctuations would directly affect species populations through catastrophic mortalities and also in many other indirect ways. If this is so, then the results of the model no longer follow.

9. The stability of the competing populations can be analysed from the community matrix. This means that assumption 1-c must hold; that is, higher order interactions must be unimportant among competing species. If these higher order interactions are important, then the whole stability analysis becomes meaningless (cf. Wilbur 1972; Neill 1974).

Applicability of the Models and Future Work on Species Packing

Although any one of assumptions 2-7 in the deterministic model or of assumptions 2-9 in the stochastic model are debilitating and may severely limit their applicability, it seems appropriate to reconsider the ability of the Lotka-Volterra equations to describe species interactions adequately. This is worthwhile because both of the models are firmly based on these equations; therefore, if they are incapable of describing multispecies interactions neither the deterministic nor the stochastic model have much utility.

Although ecologists readily admit that the Lotka-Volterra equations have several shortcomings, they often proceed to use them as a foundation upon which to build further theoretical constructs, seemingly ignoring their own objections to them. It seems apparent, however, on both theoretical (Smith 1952, 1972; Slobodkin 1963) and empirical grounds (Hairston *et al.* 1968; Wilbur 1972; Neill 1974) that the Lotka-Volterra equations cannot generally describe competitive interactions among species. Indeed, as Smith (1972) and others have pointed out, unless a system is exactly at equilibrium (and no ecosystems probably ever are), then time-lags become important in the function of the system. I can only agree with all the others who have

noted that linear equations of the Lotka-Volterra type are extremely unlikely to offer a feasible approach to the analysis of species interactions.

In addition, it should be pointed out that the stability analyses which have been employed are mainly concerned with evaluating populations near equilibrium and investigating the ability of such populations to return to the equilibrium state. Many species populations fluctuate widely, however, and are far from equilibrium (Watt 1973). Concerning these species, a more relevant concept is the persistence of populations over time. Thus, we should also be concerned with a dynamic evaluation of species populations through time, yet the classical stability analyses are not appropriate for such evaluations.

Based on the above interpretation of the two models of species packing, I conclude (1) that the approaches explored thus far are of limited utility in describing species interactions because the assumptions, both implicit and explicit, upon which the theory of species packing is based, are extremely debilitating; and (2) that further speculation within the framework of these models is unlikely to be productive. Indeed, it is interesting to note that the validity of several of the examples presented in Hutchinson's (1959) original paper on the topic have now been questioned (Grant 1972).

At this point I have no new models of species packing to present; in fact, I am not sure it is realistic to believe that a broadly applicable model of species packing can be developed. For, as Neill (1975) points out there are fundamental differences between the resource utilization patterns of vertebrates, in which juveniles utilize nearly the same types of resources as do adults, and most other organisms, in which juveniles and adults utilize different potentially limiting resources. It does appear that what is needed to develop more realistic models of species packing is more information on the importance of higher order interactions among species. Such information can be obtained using manipulation experiments and it is from this type of work that further insights into community organization are likely to emerge. For the present it seems that the complexity of species interactions severely limits the applicability of the existing mathematical models to all but the simplest (and least interesting) groups of interacting species.

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LITERATURE CITED

- Ayala, F. 1969. Experimental invalidation of the principle of competitive exclusion. *Nature* 224: 1076-1079.
- Cody, M. 1973. Character convergence. *Ann. Rev. Ecol. Syst.* 4: 189-212.
- _____. 1974. Competition and the structure of bird communities. *Princeton Monogr. Pop. Biol.* #7. 318 p.
- Culver, D. C. 1974. Species packing in Caribbean and north temperate ant communities. *Ecology* 55: 974-988.
- Darlington, P.J. Jr. 1972. Competition, competitive repulsion, and coexistence. *PNAS* 69: 3151-3155.
- Gause, G. F. 1934. *The struggle for existence.* Hafner, N.Y. 163 p.

- Grant, P. R. 1972. Convergent and divergent character displacement. *Biol. J. Linn. Soc.* 4: 39-68.
- Hairston, N. G. et al. 1968. The relationship between species diversity and stability: an experimental approach with protozoa and bacteria. *Ecology* 49: 1091-1101.
- Hespenheide, H. 1973. Ecological inferences from morphological data. *Ann. Rev. Ecol. Syst.* 4: 213-230.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *Amer. Nat.* 93: 145-159.
- MacArthur, R. H. 1969. Species packing or what competition minimizes. *PNAS* 64: 1369-1375.
- _____. 1970. Species packing and competitive equilibrium for many species. *Theor. Pop. Biol.* 1: 1-11.
- _____. 1971. Patterns of terrestrial bird communities. In D. Farner, ed. *Avian Biology I*, pp. 189-221. Academic Press, N.Y.
- _____. 1972. *Geographical Ecology*. Harper and Row, N.Y. 269 p.
- _____ and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. *PNAS* 51: 1207-1210.
- _____. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Amer. Nat.* 101: 377-385.
- May, R. M. 1973. Stability and complexity in model ecosystems. *Princeton Monogr. in Pop. Biol.* #6. 235 p.
- _____. 1974. On the theory of niche overlap. *Theor. Pop. Biol.* 5: 297-332.
- _____ and R. H. MacArthur. 1972. Niche overlap as a function of environmental variability. *PNAS* 69: 1109-1113.
- Miller, R. S. 1967. Pattern and process in competition. *Adv. in Ecol. Res.* 4: 1-74.
- Neill, W. E. 1974. The community matrix and interdependence of competition coefficients. *Am. Nat.* 108: 399-408.
- _____. 1975. Experimental studies of microcrustacean competition, community composition and efficiency of resource utilization. *Ecology* 56: 809-826.
- Popper, K. R. 1965. *Conjectures and refutations: the growth of scientific knowledge*. Harper and Row, New York, 417 p.
- Rescigno, A. 1968. The struggle for life: II, three competitors. *Bull. Math. Biophys.* 30: 291-298.
- Roughgarden, J. 1974. Species packing and the competition function with illustrations from coral reef fish. *Theor. Pop. Biol.* 5: 163-186.
- Schoener, T. W. 1974(a). Some methods for calculating competition coefficients from resource-utilization spectra. *Am. Nat.* 108: 332-340.
- _____. 1974(b). Resource partitioning in ecological communities. *Science* 185: 27-39.
- Smith, F. E. 1952. Experimental methods in population dynamics: a critique. *Ecology* 33: 441-450.
- Slobodkin, L. B. 1953. An algebra of population growth. *Ecology* 34: 513-519.
- Vandermeer, J. H. 1970. The community matrix and the number of species in a community. *Am. Nat.* 104: 73-83.
- _____. 1972. The theory of the niche. *Ann. Rev. Ecol. Syst.* 3: 103-132.
- Watt, K. E. F. 1973. Resilience and stability of ecological systems. *Ann. Rev. Ecol. Syst.* 4: 1-24.
- Wilbur, H. M. 1972. Competition, predation, and the structure of the Ambystoma-Rana sylvatica community. *Ecology* 53: 3-21.