*SPECIES PACKING, AND WHAT INTERSPECIES COMPETITION MINIMIZES**,†

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Abstract.—Species competing exclusively for renewing resources are shown to obey simultaneous differential equations equivalent to the conditions for minimizing a certain quadratic form. In this sense competition acts to select species abundances giving the best least-squares fit in an expression

$$\sum_j \frac{w_j K_j}{r_j} (r_j - S_j - x_1 a_{1j} - x_2 a_{2j} - \ldots)$$

Thus the number of species which can coexist competitively is limited mostly by the inequality of the interspecies competition coefficients and not appreciably by their magnitude. Seasonality and number of resources become the main factors limiting the number of coexisting species.

It will be shown that the abundances of a set of competing species will often be adjusted to minimize a particular expression. This is much easier to handle than the original competition equations and gives more transparent results. In particular, species packing is a clear consequence and now much more readily understood.[1]

'Competing" species whose only interaction is in their exploitation of a set of renewing resources are discussed. Only these resources are assumed to limit the competitors' growth. Similar equations could deal with predator limited competitors, but when aggression is present the explicit theory breaks down. For convenience it has been assumed that the resources do not interact, but a similar theory would cover some interacting resources.

Let x_i be the abundance of species i and obey the growth equation

$$\frac{dx_i}{dt} = c_i x_i \left[\sum_j w_j a_{ij} R_j - T_i \right] \tag{1}$$

where R_j is the abundance of resource j, w_j its weight, a_{ij} is the probability per unit time that an individual of species i encounters and eats a given unit of resource j, and c_i is a constant of proportionality, governing conversion of resources into species i. T_i is a threshold production of available food below which i decreases. The resources are themselves populations and we suppose they grow according to

$$\frac{dR_j}{dt} = \frac{r_j R_j}{K_j} \left[K_j - R_j \right] - \sum_k a_{kj} x_k R_j = \frac{r_j R_j}{K_j} \left[K_j - R_j - \sum_k \frac{K_j}{r_j} a_{kj} x_k \right]. \tag{2}$$

Here K_j is the carrying capacity of the habitat for resource R_j and a_{kj} is the same as in equation (1), because a resource eaten by x_k is removed from the resource population. r_j is defined by the equations and is usually called the

intrinsic rate of natural increase. These are the usual predator-prey equations, with a self-limitation term added to the resource equations. Near equilibrium dR_j/dt is near zero and, as long as population changes are so slow that the R's stay near equilibrium,

$$R_j = K_j - \sum_k \frac{K_j}{r_j} a_{kj}x_k.$$

Substituting this for R_j in equation (1), we find that

$$\frac{dx_i}{dt} = c_i x_i \left\{\left[\sum_j w_j a_{ij} K_j - T_i\right] - \sum_k \left[\sum_j a_{kj} a_{ij} w_j K_j / r_j\right] x_k\right\}. \tag{3}$$

This is of the form of the usual competition equations, only the terms in brackets give us an explicit expression for terms usually expressed as constants. At equilibrium with both R's and x's present and constant through time the term in braces is zero so that

$$\sum_j w_j a_{ij} K_j - T_i = \sum_k \left(\sum_j a_{ij} a_{kj} w_j K_j / r_j\right) x_k, \tag{4}$$

for all i. These, then are the conditions for competitive equilibrium. Remarkably enough, they are also the equations which result from choosing x_i to minimize[2] the single expression

$$Q = \sum_j w_j K_j / r_j (r_j - x_1 a_{1j} - x_2 a_{2j} - \ldots)^2 + 2 \sum_k T_k x_k. \tag{5}$$

To see this, we equate to zero the derivative of the expression with respect to x_i, obtaining

$$0 = -2 \sum_j w_j K_j / r_j (r_j a_{ij} - \sum_k w_j a_{ij} a_{kj} x_k) + 2T_i \tag{6}$$

for all i, which is precisely equation (4). Equation (5) says that the square of the unused production, as reflected by $\sum_j w_j K_j / r_j (r_j - \sum_k a_{kj} x_k)^2$ when added to the threshold food requirements, $2 \sum T_k x_k$, should be as small as possible. If any of the terms $r_j - \sum_k a_{kj} x_k$ is negative in this match ng, that resource, j, will vanish, so we only deal with positive values of the expression.

To relate this to species packing we revert to some more drastic assumptions. Assume T = constant and $\sum_j a_{kj}$ = constant, and let $S_j = Tr_j / \sum_j a_{kj} K_j$. This, biologically, means we are dealing with the packing of an environment by species of equal total harvesting abilities. Now we can say that equations (4) are equivalent to minimizing the simple expression

$$\sum_j \frac{w_j K_j}{r_j} (r_j - S_j - x_1 a_{1j} - x_2 a_{2j} - \ldots)^2 \tag{7}$$

for, equating to zero the derivative with respect to x_1, we get

$$0 = -2\left[\sum_j \frac{w_j K_j}{r_j} a_{1j} (r_j - S_j) - \sum_k \left(\sum_j \frac{w_j K_j}{r_j} a_{1j} a_{kj}\right) x_k\right]$$

which is just equation (4) for $i = 1$. The same is true for each i. Hence under these simple conditions[3] competition minimizes expression (7) which says it

adjusts $x_1, x_2, \ldots$, so that $\sum_k a_{kj}x_k$ is the best least squares fit to the value $r_j - S_j$. For any given set of species, $\sum_k a_{kj}x_k$ will be greater than $r_j - S_j$ for some intervals of j and less for others. Where it is greater, no invader can improve the fit and where it is less an invader will improve the fit and hence be admitted. This means that no community of the type we discuss is ever fully saturated even with species of constant niche breadth unless by some chance the $\sum a_{kj}x_k$ are a perfect fit. However there are species clusters within each community which will prevent invasion. Thus each community will resist invasion by some phenotypes but always be vulnerable to others. Of course complete resistance to invasion may be achieved for other reasons: When the $\sum a_{kj}x_k$ curve fits $r - S$ so closely that an invader needs less than one-half individual to optimize the fit, the addition of one would make it worse. (Realistically it will resist invasion unless there are opportunities for a substantial propagule of a new species.) Of more interest is the effect of seasonal fluctuations in the r_j values. In this case invasibility at one season is not sufficient; the invader must improve the fit at all seasons. Plausibly for a suitably large number of species a fluctuation in r_j will mean no species can invade at every season, and hence allow saturation. There will also be saturation if the number of species exceeds the number of resources, or if no suitable invader happens to be present.

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† The result of the present paper extends that of Mac Arthur and Levins to packing in non-uniform environments and that of Schoener by showing with what measures of resource production and utilization his heuristic scheme is valid.

[1] For previous discussions of species packing see Mac Arthur, R., and R. Levins, *Amer. Nat.*, **101**, 377 (1967); Schoener, T., *Evolution*, **19**, 189 (1965); and Levins, R., *Evolution in Changing Environments* (Princeton University Press, 1968).

[2] The equations only require that we find the stationary value of equation (5), but, for biological reasons, only the minimum is realistic. With Q as in equation (5), equation (3) can be written:

$$\frac{dx_i}{dt} = -\frac{x_i c_i}{2}\frac{\partial Q}{\partial x_i}$$

whence

$$\frac{dQ}{dt} = \sum_i \frac{\partial Q}{\partial x_i}\frac{dx_i}{dt} = -\frac{1}{2}\sum x_i c_i \left(\frac{\partial Q}{\partial x_i}\right)^2,$$

which must be negative. Hence Q is minimized and the equations are stable. (The author is indebted to M. Kimura for this interpretation.)

[3] The expression in equation (5) is minimized under much more general conditions, for as long as competition acts by individuals of two species being in the same place at the same time, equation (3) will take the form

$$\frac{dx_i}{dt} = c_i x_i \left[G_i - \sum_k \left(\sum_j w_j p_{ij} p_{kj} \right) xk \right]$$

and the expression minimized takes the form

$$Q = \sum_j w_j \left(\sum_k p_{kj} x_k\right)^2 - 2\sum G_k x_k.$$

If time lags and age distributions enter, their effect is unknown.