Reports

Interspecific Competition: A New Approach to the Classical Theory

Abstract. *The biological consequences of the classical theory of competition are shown to be at least partly a function of a very special way of interpreting particular constants in simple equations. It is shown how altered consequences may be obtained by different, but equally plausible, interpretations of those constants.*

The interaction between two competing populations has frequently been represented by a set of two differential equations, in which the per capita rate of population growth is a function (F) of the population densities (N) of both species, that is, $dN_i/N_i dt = F_i(N_1 N_2)$, for $i = 1,2$. The usual procedure in theoretical ecology is to let F be linear (*1*). A simple equilibrium analysis of such equations leads to qualitative predictions about the process of competition, predictions which have at times been raised to the level of ecological law.

Critics of this approach seem to have concentrated on the linearity assumption. Perhaps this is not as important an assumption as is widely believed, since the generalized system is expected to behave almost linearly near equilibrium (*2*). Whether any natural system actually approaches an equilibrium is, of course, quite another question. While I readily acknowledge problems associated with the linear assumption, I offer here a different criticism of the way in which the theoretical literature treats the analysis of competition. A reexamination of classical theory reveals that some well-known general predictions are merely artifacts of interpreting certain well-defined parameters too broadly. Furthermore, I suggest that a more strict interpretation of such parameters leads to even more general predictions, most of which are supported by casual observation, or the conventional wisdom of field biologists.

Classical approach. Assuming that F is linear, we have

$$\frac{dN_i}{N_i dt} = r_j - a_{ii}N_j - a_{ij}N_j \qquad (1)$$

for $i = 1,2$. If species j is absent the population density of species i (N_i) will tend to the value r_i/a_{ii}, which is usually called the carrying capacity and symbolized by K_i (that is, for $t \to \infty$, $\lim N_i = r_i/a_{ii} = K_i$).

The intensity of interspecific competition is normally expressed as "the change in the per capita growth rate of species *i*, due to the presence of an individual of species *j*, relative to the change in per capita growth rate of species *i*, due to the presence of an individual of species *i*," and symbolized by α_{ij}

$$\frac{\partial(dN_i/N_i dt)/\partial N_j}{\partial(dN_i/N_i dt)/\partial N_i} = \frac{a_{ij}}{a_{ii}} = \alpha_{ij}$$

That is, the interspecific effect of one species is expressed as a fraction of the intraspecific effect of the other species. Substituting α_{ij} and K_i into Eq. 1 we obtain the familiar form

$$\frac{dN_i}{dt} = r_i N_i \frac{K_i - N_i - \alpha_{ij}N_j}{K_i} \qquad (2)$$

which lends itself well to obvious and manifestly reasonable biological interpretations (*1, 3*). In abstract terms, Eq. 2 implies that (i) there is enough "space" in the environment for K_i individuals of species *i* alone, (ii) a portion α_{ij} of that space is taken up by each individual of species *j*, and (iii) the per capita rate of growth of species *i* is a direct function of the proportion of the space not yet utilized.

Excepting the trivial case of both species having zero population densities, the only point at which both species are at equilibrium ($dN_i/dt = 0$; $i = 1,2$) is that which satisfies the equation $N_i = K_i - \alpha_{ij}N_j$, for $i = 1,2$. Using standard stability analysis (*4*), it can be shown that this equilibrium point is stable if and only if $\alpha_{ij}\alpha_{ji} < 1$. If $\alpha_{ij}\alpha_{ji} < 1$ the two species are said to be α-compatible (*5*). If $K_1 < K_2/\alpha_{21}$ and $K_2 < K_1\alpha_{12}$ or $K_1 > K_2/\alpha_{21}$ and $K_2 > K_1/\alpha_{12}$, the value of N_i at the singularity will be positive for $i = 1,2$, and the two species are said to be K-compatible (*6*). For both species to persist indefinitely, they must be both α- and K-compatible; that is

$$K_1 < K_2/\alpha_{21} \qquad (3a)$$

$$K_2 < K_1/\alpha_{12} \qquad (3b)$$

Equations 3a and 3b are graphed in Fig. 1A. If the two species are not α-compatible we obtain either an indeterminate solution (metastable, or saddle

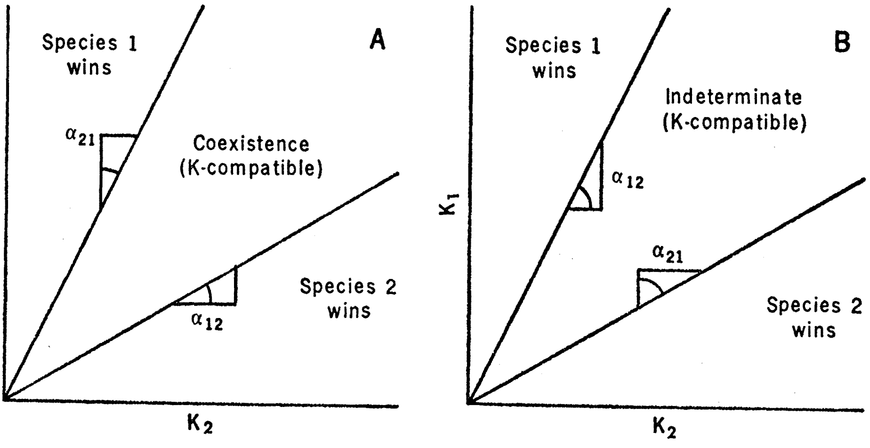

Fig. 1. Equations 3a and 3b plotted in K_1,K_2 space. (A) represents the condition of α-compatibility ($\alpha_{ij}\alpha_{ij} < 1$). In both (A) and (B) the lines are the equations $\alpha_{21}K_1 = K_2$ and $\alpha_{12}K_2 = K_1$. The area above both lines is the set of all pairs of K's for which species 1 drives species 2 to extinction. The area below both lines is the set of all pairs of K's for which species 2 drives species 1 to extinction. The area between the two lines is the set of all pairs of K's for which either the two species will coexist (A) or the outcome of competition is indeterminate (B).

point) or a monospecific solution (see Fig. 1B).

An often cited conclusion from this analysis is that the intrinsic rate of natural increase, r, does not appear in the stability analysis, or biologically, the outcome of competition is totally independent of the population growth rate of each of the species.

Alternative interpretation. Recalling that $K_i = r_i/a_{ii}$, we may recast Eq. 3a and 3b as

$$r_1/a_{11} < \frac{r_2/a_{22}}{a_{21}/a_{22}}$$

$$r_2/a_{22} < \frac{r_1/a_{11}}{a_{12}/a_{11}}$$

On simplification we obtain

$$r_1\frac{a_{21}}{a_{11}} < r_2$$

$$r_2\frac{a_{12}}{a_{22}} < r_1$$

as the conditions for both α- and K-compatibility. Note that the coefficient which multiplies r on the left-hand side of these equations has a simple biological interpretation, namely, "the change in the per capita growth rate of species i, due to the presence of an individual of species j, relative to the change in the per capita growth rate of species j, due to the presence of an individual of species j"

$$\frac{\partial(dN_i/N_i dt)/\partial N_j}{\partial(dN_j/N_j dt)/\partial N_j} = \frac{a_{ij}}{a_{jj}} = \beta_{ij}$$

That is, instead of comparing interspecific competitive ability (a_{ij}) to the intraspecific competitive ability of the other species (a_{ii}), we compare it to that of the species perpetrating the competition (a_{jj}). Stability conditions can be restated in the new notation. The equilibrium will be stable if and only if $\beta_{12}\beta_{21} < 1$, and both species will persist indefinitely at positive densities if and only if

$$\beta_{21}r_1 < r_2 \quad (4a)$$

$$\beta_{12}r_2 < r_1 \quad (4b)$$

Table 1. Necessary qualitative relations among various parameters in the basic equations. See text for fuller explanation.

Parameter			
α	β	r	K
?	$\beta_{ij} << \beta_{ji}$	$r_i < r_j$	?
?	$\beta_{ij},\ \beta_{ji} \rightarrow 1$	$r_i \approx r_j$	?
$\alpha_{ij} << \alpha_{ji}$	?	?	$K_i < K_j$
$\alpha_{ij},\ \alpha_{ji} \rightarrow 1$	?	?	$K_i \approx K_j$

Equations 4a and 4b are graphed in Fig. 2.

When competition is defined in this way, r is not irrelevant to the outcome of competition. Clearly, the biological result depends on the interpretation of the constants in the original equations—specifically, on which of the constants are thought to be fixed and which are allowed to vary. In the classical analysis, r, K, and α are assumed to vary independently of one another. Thus if we wish to hold r_1 and α_{12} constant and see what might be the effect of varying K_1, we must in fact vary a_{11} (since $K_1 = r_1/a_{11}$). But varying a_{11} implies that a_{12} must also be changed, to keep α_{12} invariant. Is it not as valid to suppose that β_{12} is invariant? The point is simply that the parameters in Eq. 1 may be manipulated in a variety of ways, depending on what is thought to be biologically reasonable. The classical formulation presumes that there is some underlying biological reason to suppose that a_{ij} and a_{ii} are coupled so that their ratio is always constant. Perhaps it could be argued that such an assumption is more reasonable when made about the ratio a_{ij}/a_{jj}, but I merely wish to point out that such an assumption is equally reasonable.

Discussion. The above analysis makes it clear that the independence of r and competitive outcome is artifactual, and suggests that the independence of K and competitive outcome makes as much sense, if not more. In general, qualitative generalizations about competitive ability cannot always be made without exactly specifying what is meant by competitive ability. Yet when ecologists speak of competitive ability it is usually not at all clear whether they are talking about σ_{ij}, β_{ij}, or a_{ij}.

More importantly, the above framework suggests a diverse set of qualitative predictions. The parameters in the model are constrained in certain ways so as to suggest certain correlations to be sought in nature. These predicted correlations are more or less summarized in Table 1. Such predictions are made possible by precisely defining what is meant by phrases such as competitive ability or competitive intensity.

Consider a situation in which $\beta_{ij} << \beta_{ji}$, a situation summarized in row 1 of Table 1. This condition requires no particular configuration of the α's or K's, but implies that $r_i < r_j$. Qualitatively if one species is much better at "β-competition" than a second species, the second species must have a larger intrinsic growth rate than the first, if they are to coexist. Thus it is reasonable to search in nature for a correlation between competitive ability and intrinsic growth rate, if competitive ability is viewed in the β sense. Note that this predicted correlation is not based on an evolutionary argument, but derives from ecological dynamics only.

Next consider both β coefficients near unity, as summarized in row 2 of Table 1. Such a situation requires relative equality between r_1 and r_2 in order to achieve coexistence, but implies nothing whatsoever about the values of α and K. This is a particularly interesting consequence since $\beta \rightarrow 1$ implies that both species have similar requirements, since $\beta = 1$ means that the interspecific effect is the same as the intraspecific effect. Thus, as two species distinguish one another less and less, in terms of the way in which one individual depresses

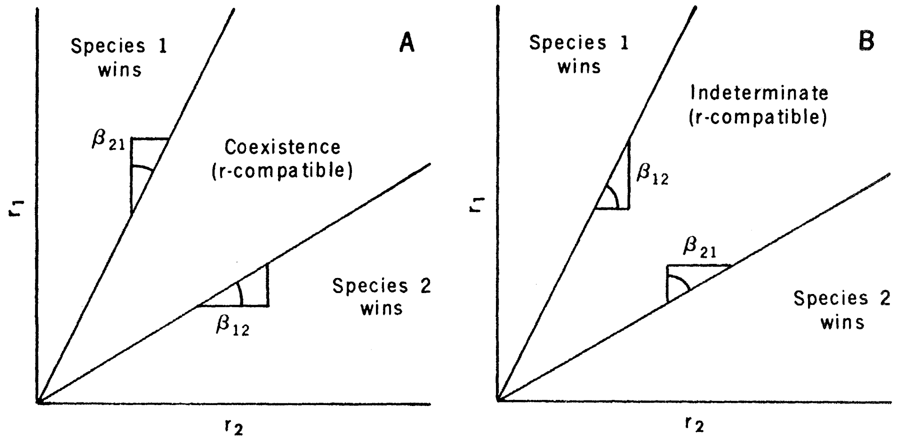

Fig. 2. Equations 4a and 4b plotted in r_1,r_2 space. (A) represents the condition of β-compatibility ($\beta_{ij}\beta_{ji} < 1$). In both (A) and (B) the lines are the equations $\beta_{21}r_1 = r_2$ and $\beta_{12}r_2 = r_1$. The area above both lines is the set of all pairs of r's for which species 1 drives species 2 to extinction. The area below both lines is the set of all pairs of r's for which species 2 drives species 1 to extinction. The area between the two lines is the set of all pairs of r's for which either the two species will coexist (A) or the outcome of competition is indeterminate (B).

the survivorship and fecundity of other individuals, their intrinsic rates must become more and more equal. Loosely, we expect ecological equivalents to coexist only if their *r*'s are relatively equal.

A symmetrical situation exists in row 4 of Table 1. If $\alpha \rightarrow 1$, it is necessary for $K_i \approx K_j$ for the species to coexist. That is, as two species distinguish one another less and less, their carrying capacities must become more and more equal for coexistence. Again we might loosely state that ecological equivalents can only coexist if their *K*'s are relatively the same.

A somewhat paradoxical situation exists here, since coexistence of ecological equivalents requires on the one hand similar intrinsic rates (*r*'s) and on the other hand similar carrying capacities (*K*'s). Clearly we are dealing with two distinct concepts of ecological equivalents. Ecological equivalents in the sense of $\alpha \rightarrow 1$ implies that the received effects of competition are the same for both species. Ecological equivalents in the sense of $\beta \rightarrow 1$ implies that the imposed effects of competition are the same for both species.

Finally, suppose $\alpha_{ij} << \alpha_{ji}$, as summarized in row 3 of Table 1. This time nothing can be said about the values of r and β (the classic situation), but $K_j > K_i$ is necessary if coexistence is to be likely.

In summary, the textbook approach to competition theory has ignored a reasonable interpretation of the meaning of competition. This oversight has led to a somewhat restricted view of the role of competition in nature, including the widespread belief that the qualitative outcome of competition is not dependent on the values of the intrinsic rates of natural increase. The analysis presented here indicates that this is not, in fact, a general result, but stems from a limited interpretation of simple equations. When the notion of β-competition is introduced, r becomes important in determining the outcome of competition. Furthermore, it is possible to suggest a negative correlation between competitive ability and the intrinsic rate of natural increase for species coexisting in nature.

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References and Notes

1. See any ecology text, such as J. M. Emlen, *Ecology: An Evolutionary Approach* (Addison-Wesley, Reading, Mass., 1973); R. E. Ricklefs, *Ecology* (Chiron, Portland, Ore., 1973); E. R. Pianka, *Evolutionary Ecology* (Harper & Row, New York, 1974).
2. R. W. May, *Stability and Complexity in Model Ecosystems* (Princeton Univ. Press, Princeton, N.J., 1973).
3. G. J. Gausse, *The Struggle for Existence* (Williams & Wilkins, Baltimore, 1934).
4. A. Blaquière, *Nonlinear System Analysis* (Academic Press, New York, 1966); R. Rosen, *Dynamical System Theory in Biology* (Wiley-Interscience, New York, 1970).
5. J. F. Riebesell, *Ecology* **55**, 183 (1974).
6. J. H. Vandermeer, *Am. Nat.* **104**, 73 (1970).
7. This report was prepared in consultation with D. Boucher, D. Culver, W. Durham, K. Frogner, L. Real, V. Sork, R. Westman, and the students of Zoology 457 at the University of Michigan.

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Alaskan Thermokarst Terrain and Possible Martian Analog

Abstract. *A first-order analog to martian fretted terrain has been recognized on enhanced, ERTS-1 (Earth Resources Technology Satellite) imagery of Alaskan Arctic thermokarst terrain. The Alaskan analog displays flat-floored valleys and intervalley uplands characteristic of fretted terrain. The thermokarst terrain has formed in a manner similar to one of the processes postulated for the development of the martian fretted terrain.*

Earlier investigators have discussed the possible occurrence and characteristics of subsurface ice on Mars in connection with the occurrence of chaotic and fretted terrains (*1*, *2*). We have examined ERTS-1 (Earth Resources Technology Satellite) imagery of the area around the Ikpikpuk and Price rivers in northern Alaska and have recognized an Alaskan Arctic thermokarst terrain that appears to be a close analog to the martian fretted terrain identified in the imagery of Mariner 9.

Figure 1 is a Mariner 9, narrow-angle (camera B) frame illustrating the principal features of martian fretted terrain. It shows relatively smooth and flat lowlands with gentle undulations, several scattered craters of recent origin, and a few locally rough areas. The lowlands are bordered in general by abrupt arcuate escarpments 0.5 to 2.0 km in height. The total extent of fretted terrain is estimated to be approximately 4.75×10^6 km^2 (3 percent of the planet's surface) (*2*). One of the processes postulated for the development of fretted terrain is the collapse of upland, cratered terrain. A possible mode of origin suggested by several investigators is the degradation of massive ground ice. However, skeptics have questioned the possibility of sufficient quantities of massive subsurface ice and it has been pointed out that no terrestrial analogs are known (*2*).

Owing to a fortunate coincidence of low sun angle and a uniform snow cover, we have been able to recognize what appears to be a close terrestrial analog in the ERTS-1 multispectral imagery of an area separating the Arctic coastal plain from the foothills of the Brooks Range in northern Alaska. Snow cover masks the vegetation patterns and the numerous thaw lakes. Enhancement techniques highlight the relief (1 to 30 m) (*3*) existing between flat-floored thermokarst depressions and northeast-southwest trending, intervalley uplands.

Figure 2 is a 9500-km^2 portion of an ERTS-1 multispectral scanner (MSS), band 7, enhanced image (ID 1237-21353) of this area. A linear contrast stretch and geometric corrections identical to those done on the imagery of the Mariner 6, 7, and 9 missions were carried out by the Image Processing Laboratory (IPL) of the Jet Propulsion Laboratory (*4*). This processing was applied to images taken in MSS spectral bands 4 (0.5 to 0.6 μm), 5 (0.6 to 0.7 μm), 6 (0.7 to 0.8 μm), and 7 (0.8 to 1.1 μm). The contrast stretch was done to enhance the tonal differences of this uniformly high-albedo image. The geometric correction merely skewed the image to compensate for the earth's motion under the satellite during image acquisition. Subsequent inspection showed that the enhancement of band 7 gave the best rendition of this scene. Figure 3 is an enlarged portion of the thermokarst area in Fig. 2. This enlargement (× 4) facilitates comparison of some of the features common to the terrains shown in Figs. 1 and 2.

Terrestrial thermokarst topography consists of pits, basins, valleys, and closed depressions with small hummocks often containing lakes (*5*). This topography is characteristic of degrading permafrost areas with high subsurface ice contents; as the ice melts, the surface collapses. Local forms of thermokarst topography depend on the amounts and configuration of the subsurface ice and the balance between thermal, mechanical, and fluvial erosion. The slumping can occur along a slope or cliff by slope recession (*6*) and in flat areas by subsidence upon removal of subsurface ice. This slumping process is characterized by the retreat