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Competitive Exclusion

The exclusion principle is recast in the context of a generalized scheme for interspecific interactions.

Bernard C. Patten

The colloquy in these pages (*1*) concerning the newly denominated but ancient theory of "competitive exclusion" has generated a controversy which appears to have resulted in a standoff. One wonders if the reason may not be implicit in A. N. Whitehead's remarks when he admonished his contemporaries for living off the intellectual capital accumulated in the 17th century, warning that any culture was doomed which could not throw off the inertia of habitual thinking and burst through the facade of its own concepts. Exclusion theory is controversial, it would seem, not so much because it isn't intuitionally reasonable or, for the most part, empirically expressed, but rather because it is couched in an archaic context of 19th-century dogma within which circular reasoning is the only alternative to progress (in terms acceptable to modern apprehension of scientific episteme). This circularity is reflected in the earliest and latest formulations of the exclusion principle:

> . . . it is the most closely-allied forms—varieties of the same species, and species of the same genus or related genera—which, from having nearly the same structure, constitution and habits, generally come into severest competition with each other; consequently, each new variety or species, during the progress of its formation, will generally press hardest on its nearest kindred, and tend to exterminate them. [Darwin, 1859]
>
> [Since] complete competitors cannot coexist . . . ecological differentiation is the necessary condition for coexistence. [Hardin, 1960]

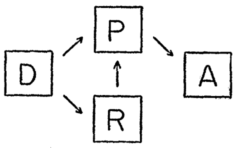
Thus the total achievement of a century of thought amounts to providing the contrapositive of the original proposition.

The exclusion principle is regarded in this article as a legacy from the past, whose continued recognition at "law" status can only interfere with a healthy development of concepts whose further disquisition it tends to block. Therefore it should be relegated as prudently and expeditiously as possible to a de-emphasized position in a broader, more modern framework. A tentative step in this direction is provided, which casts exclusion in a context which includes also the cooperative aspects of interspecific phenomena. Strong reliance on cybernetic models as formulated by Ashby (*2*) is acknowledged.

Consider a universe Υ of entropy states, some at higher and others at lower levels of potential. Discrete enclaves of high potential (the sun for example) represent sources of unconstrained variety (information, negentropy) which transmit to low-potential sinks comprising states of maximally constrained variety (entropy). Let the subset υ represent the biological states in Υ at intermediate potentials. This collectivity, consisting of states of partially constrained variety, possesses the capacity to impose constraint upon information and so to generate entropy—an accomplishment, as will be shown, which requires an information store which υ seeks to maintain (and extend) contrary to the gradient of potential. The situation is analogous to a two-person von Neumann game of the non-zero-sum type (*3*) in which υ simultaneously seeks to gain information from Υ for use in blocking its gain of information from Υ. Solution of this paradox constitutes the fundamental problem of regulation. Two basic principles are involved: the law of entropy and the law of requisite variety. These laws are best discussed against a background of the nature of υ's organization.

Consider, as a functional element of υ, "species" A, which regulates a set of essential variables within a favorable range α beyond which A fails to survive. The subset α corresponds to a Hutchinsonian niche (*4*). Disturbances D, in the form of information from the environment Υ, threaten to drive the states of A outside of α. If D may be visualized as acting through some dynamic system P, a protocol characteristic of Υ, then the initial diagram of immediate effects takes the form

A forms another dynamic system R, a regulator which can be coupled to P to produce a machine capable of blocking the flow of variety to the essential variables:



The "game" takes the following sequence: (i) the environment Υ makes an arbitrary move D; (ii) R assumes a value determined by D's value; and

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The author is associate professor of marine science, College of William and Mary, at the Virginia Institute of Marine Science, Gloucester Point.

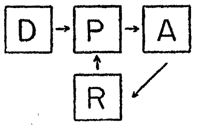
(iii) P determines the outcome which is or is not in α. The process is incessant, and the sequence of events constituting the "life" of any discrete informational unit a of A may be represented as

$$D_1\ a_1\ D_2\ a_2\ D_3\ .\ .\ .$$

—a sequence which continues until a falls outside of α. It is noteworthy that A's regulation need not be perfect; it only has to be "good enough" (and, disturbingly, the a's are freely expendable).

"Good enough" regulation may be of two kinds: a priori and a posteriori. In the former, D and R act simultaneously on P to produce a state change in A. The strategy of this defense against variety is that of a gambler—playing the odds. A regulator of limited capacity is employed to handle variety within a certain fixed range (say, for example, three standard deviations). This is cheap regulation, and when D exceeds the range of R's effectiveness, the essential variables fall beyond α and many or all of the a's fail to survive. This kind of regulation is commonplace in biology, and disturbances of uncommon magnitude lead to "cycles" of rarity and abundance, and to such catastrophic phenomena as mass mortalities. Essential to a program of a priori regulation is a residuum of variety stored in very effective (n standard deviations) regulators, such as resistant seeds and spores, to function as information sources for repopulation when the D's return again to normal levels.

Regulation a posteriori is much more sophisticated, and the entity regulated has far more integrity and is far less expendable. This is error-controlled regulation in which D produces, through P, a perturbation in A, which then transmits information concerning its displacement to R, which then acts on P to correct the error in A's trajectory. Like a priori regulation, this control by negative feedback is not perfect; in fact, the method relies on error. Perfect control in this case corresponds to no control! A diagram of immediate effects



illustrates the closed loop $ARPA$.

Regulation by error is most keenly developed in the higher behavioral phenomena of higher organisms, but it is also important, although more subtle, at the ecological level. An excellent example is provided by Cruikshank's data on the abundance of three species of warbler in successive years in Maine, cited by MacArthur (*5*). The trajectories (where i represents increased abundance over the preceding year, and d, decrease) were

Myrtle	*didiiiddididi*
Black-throated green	*iidididdidi*
Blackburnian	*idiididididd*

for which the corresponding matrices of transition probabilities are

Myrtle

$$\begin{array}{c|cc} \downarrow & d & i \\ \hline d & .17 & .67 \\ i & .83 & .33 \end{array}$$

Black-throated green

$$\begin{array}{c|cc} \downarrow & d & i \\ \hline d & .20 & .80 \\ i & .80 & .20 \end{array}$$

Blackburnian

$$\begin{array}{c|cc} \downarrow & d & i \\ \hline d & .20 & .83 \\ i & .80 & .17 \end{array}$$

These matrices show clearly that each species of warbler tends to increase when it is rare and to decrease when it is common, a neat illustration of feedback control at the population level.

Laws Basic to Regulation

Let us return now to the two laws basic to regulation—the entropy law and the law of requisite variety. As discussed earlier, external variety can only be blocked by internal variety supplied to a regulator. The law of requisite variety (*2*) fixes exactly the amount of regulation achievable by establishing the lower limit to which A's variety can be depressed; it is

$$\frac{D\text{'s variety}}{R\text{'s variety}}$$

This principle is isomorphic with Shannon's (*6*) theorem 10 concerning the data-handling capacity of correction channels. For a given D, therefore, R's variety must be commensurately high in order for A's states to be constrained within α. Should A falter in providing the necessary information when it is needed, it fails to survive—that is, it ceases to continue as a functional entity of υ. The entropy law, a general principle of which the second law of thermodynamics is but a particular expression, works against A's regulatory efficacy by passively providing the gradient against which required variety must be accumulated. That this law operates automatically as soon as convergence occurs in a transformation is shown by the following transformation:

$$T\colon\ \downarrow\ \begin{matrix} M & N & O \\ N & O & O \end{matrix}$$

in which the operand has a variety of 1.6 bits per element ($-3/3 \log_2 1/3$) and the transform a variety of 0.9 bits per element ($-1/3 \log_2 1/3 - 2/3 \log_2 2/3$). A second application of operator T produces a variety of zero, the maximum entropy condition.

A more concrete example may be obtained from biochemistry. When, in the tricarboxylic acid cycle, succinate is transformed to fumarate, some 36 kilocalories per mole are liberated, representing an entropy gain which cannot be reversed *within* the limited framework of the Krebs system. For the cycle to continue, new variety in the form of pyruvate from the glycolytic chain must be provided. This comes, ultimately, from Υ.

The foregoing conditions under which A must preserve its integrity are basic to the following proposition, upon which an approach to the competitive exclusion concept may be based. The proposition, a suggested working hypothesis, is that selective advantage accrues to those elements of υ which regulate best, in the sense of achieving unit stability at the lowest cost in information. We shall examine interspecific phenomena in relation to this hypothesis.

Let us consider another species, B, having niche β. Several relationships are possible between A and B. If the phase spaces α and β have no points in common in space and time, A and B are completely independent. But when the niches overlap to some degree spatially and temporally, the species interact, which is to say that their components become coupled to form a new machine AB of epispecific proportions. A biocenose—that is, an ecological community Γ—may be regarded as a large functional element of υ made up of the combined coupling of numerous species with intersecting niches ($\Gamma = AB\ .\ .\ .\ Z$). Hence Γ, like each of its components, is itself a self-regulating device which strives to maintain at lowest possible cost *its* essential variables within a favorable range $\gamma\,(\alpha\,\beta\ .\ .\ .\ \zeta)$. Competition, and the antithesis cooperation, may be defined in terms of the total success of

Γ in meeting that goal. If efficacy in regulation of any coupling *AB* is greater than the combined efficacy of its elements before interaction (that is, $A + B$), then the interaction is favorable—cooperative—and will tend to be perpetuated. Cooperative interactions generally occur when *A* and *B* are only remotely related—that is, when α and β do not overlap appreciably. When niches are similar, however, a couplet may prove to have reduced regulatory capacity, and Γ tends to revert to a more favorable state by eliminating one of the competitors—the one which, functioning separately, is the least effective regulator. This is the exclusion principle—a modern expression of the "struggle for existence."

Experimental Evidence

The best experimental evidence for the validity of the theory has been provided by the work of Thomas Park and his colleagues (*7*) with flour beetles. In every experiment in which two closely allied species of beetle were forced to cohabit a limited environment, one of the species survived while the other was eliminated. In a given experimental situation, however, it was not always the same species which survived. But (and this is of the utmost significance) the species surviving most often was the one which sustained higher densities when grown alone under conditions of temperature and humidity identical to those for the other species. An exception to this rule was observed in treatment 5 (*7*), in which the species which survived most often in competition was the one which, grown alone, maintained the lower density. A possible explanation for this, and also for the seemingly stochastic nature of the general result (only at the environmental extremes did the same species win every contest) may be that a "head count" is probably a pretty crude measure of variety.

Cole, in his rebuttal to Hardin's exposition of competitive exclusion (*1*), stated, "No two species can remain sympatric indefinitely whether or not they compete." Park and his coworkers did not rule out this consideration in the case of the *Tribolium* model. When the model is viewed as a Markovian machine, the prediction is that over an infinitely long time either the beetles must succumb or their population must grow to infinity. Comparing this with the experimental results (maximum duration 1860 days), Park and his associates conclude that either (i) the probabilities of growth, death, and passage from state A_i to A_{i+1} do not depend solely upon the state of the operand but depend also on the history of the population prior to A_i, or (ii) the period of observation was much less than infinite. The authors "guess" in favor of the second alternative; their position is strengthened by the fact that the first is cybernetically unsound: any transition depends only on the state of the operand at the time the operator acts. The fact that exclusion always occurred in a short time relative to the total potential life of each culture indicates that the *ultimate* disappearance of an element *A* from the community Γ as the normal consequence of the latter's evolution toward a more favorable position with respect to the working hypothesis is inadmissible as an argument against competitive exclusion.

Let it be noted in conclusion that nothing in the cybernetic model presented precludes the possibility of passive coexistence between *A* and *B*. As a matter of fact, if competitive interaction lies at one coupling extreme and cooperation at the other, then what is more natural than that at some point intermediate in the continuum there be a coupling in which *AB* is neither less nor more effective in total regulatory capacity than $A + B$? Hence, such models as Skellam's describing coexistence (*8*) are not necessarily incompatible with the exclusion principle.

Summary

Two species, *A* and *B*, interact when their niches α and β intersect in space and time. The composite element *AB* may be either more, less, or equally effective in regulation. It is suggested that the first condition exists when the overlap between α and β is small; this leads, on a large scale, to complex biocenotic phenomena in which components of a tremendously diversified biota may coexist. The coupling *AB* is likely, on the other hand, to be antagonistic to optimization of regulation by the whole community; in this case, it is postulated, one of the components (the less effective regulator acting alone) is purged. This is competitive exclusion, and it develops when α and β intersect greatly. Between these extremes of cooperation and competition lies an area of niche intersection in which *AB* is not much better or worse than *A* or *B* alone. This case gives rise to passive coexistence of *A* and *B*. These are the extremes; even a cursory consideration of the permutational possibilities for niche intersection gives an immediate concept of the overwhelming variety of possible interspecific interactions and a glimpse of the dangers inherent in overemphasizing a single aspect. It is therefore advocated that the principle of competitive exclusion be regarded as only a small segment of a broad class of interspecific phenomena (*9*).

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