The Competitive Exclusion Principle

Author(s): Garrett Hardin

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parameters have values typical of, say, any warm, moist air mass found in spring and summer in the central United States, with a single exception, a quantity K called *circulation,* which is a measure of the general rotation of the air in which the tornado is imbedded. This quantity has been estimated with great accuracy for at least one tornado, and I think we know very closely its value in the typical case. It corresponds, however, to so great a rotation that it is obviously a very rare occurrence. This may explain the infrequency of tornadoes. It is possible that we could learn to predict this (parent) small-scale cyclone, and this in turn could lead to better forecasting of tornadoes.

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The Competitive Exclusion Principle

An idea that took a century to be born has implications in ecology, economics, and genetics.

Garrett Hardin

On 21 March 1944 the British Ecological Society devoted a symposium to the ecology of closely allied species. There were about 60 members and guests present. In the words of an anonymous reporter (*1*), "a lively discussion . . . centred about Gause's contention (1934) that two species with similar ecology cannot live together in the same place. . . . A distinct cleavage of opinion revealed itself on the question of the validity of Gause's concept. Of the main speakers, Mr. Lack, Mr. Elton and Dr. Varley supported the postulate. . . . Capt. Diver made a vigorous attack on Gause's concept, on the grounds that the mathematical and experimental approaches had been dangerously over simplified. . . . Pointing out the difficulty of defining 'similar ecology' he gave examples of many congruent species of both plants and animals apparently living and feeding together."

Thus was born what has since been called "Gause's principle." I say "born" rather than "conceived" in order to draw an analogy with the process of mammalian reproduction, where the moment of birth, of exposure to the external world, of becoming a fully legal entity, takes place long after the moment of conception. With respect to the principle here discussed, the length of the gestation period is a matter of controversy: 10 years, 12 years, 18 years, 40 years, or about 100 years, depending on whom one takes to be the father of the child.

Statement of the Principle

For reasons given below, I here refer to the principle by a name already introduced (*2*)—namely, the "competitive exclusion principle," or more briefly, the "exclusion principle." It may be briefly stated thus: *Complete competitors cannot coexist.* Many published discussions of the principle revolve around the ambiguity of the words used in stating it. The statement given above has been very carefully constructed: every one of the four words is ambiguous. This formulation has been chosen not out of perversity but because of a belief that it is best to use that wording which is least likely to hide the fact that we still do not comprehend the exact limits of the principle. For the present, I think the "threat of clarity" (*3*) is a serious one that is best minimized by using a formulation that is *admittedly* unclear; thus can we keep in the forefront of our minds the unfinished work before us. The wording given has, I think, another point of superiority in that it seems brutal and dogmatic. By emphasizing the very aspects that might result in our denial of them were they less plain we can keep the principle explicitly present in our minds until we see if its implications are, or are not, as unpleasant as our subconscious might suppose. The meaning of these somewhat cryptic remarks should become clear further on in the discussion.

What does the exclusion principle mean? Roughly this: that (i) if two noninterbreeding populations "do the same thing"—that is, occupy precisely the same ecological niche in Elton's sense (*4*)—and (ii) if they are "sympatric"—that is, if they occupy the same geographic territory—and (iii) if population A multiplies even the least bit faster than population B, then ultimately A will completely displace B, which will become extinct. This is the "weak form" of the principle. Always in practice a stronger form is used, based on the removal of the hypothetical character of condition (iii). We do this because we adhere to what may be called the axiom of inequality, which states that no two things or processes,

The author is professor of biology at the University of California (Santa Barbara), Goleta. This article is based on a Darwin centennial lecture given before the Society for the History of Medical Science of Los Angeles on 24 November 1959.

in a real world, are precisely equal. This basic idea is probably as old as philosophy itself but is usually ignored, for good reasons. With respect to the *things* of the world the axiom often leads to trivial conclusions. One postage stamp is as good as another. But with respect to competing *processes* (for example, the multiplication rates of competing species) the axiom is never trivial, as has been repeatedly shown (*5–7*). No difference in rates of multiplication can be so slight as to negate the exclusion principle.

Demonstrations of the formal truth of the principle have been given in terms of the calculus (*5, 7*) and set theory (*8*). Those to whom the mathematics does not appeal may prefer the following intuitive verbal argument (*2*, pp. 84–85), which is based on an economic analogy that is very strange economics but quite normal biology.

"Let us imagine a very odd savings bank which has only two depositors. For some obscure reason the bank pays one of the depositors 2 percent compound interest, while paying the other 2.01 percent. Let us suppose further (and here the analogy is really strained) that whenever the sum of the combined funds of the two depositors reaches two million dollars, the bank arbitrarily appropriates one million dollars of it, taking from each depositor in proportion to his holdings at that time. Then both accounts are allowed to grow until their sum again equals two million dollars, at which time the appropriation process is repeated. If this procedure is continued indefinitely, what will happen to the wealth of these two depositors? A little intuition shows us (and mathematics verifies) that the man who receives the greater rate of interest will, in time, have all the money, and the other man none (we assume a penny cannot be subdivided). No matter how small the difference between the two interest rates (so long as there is a difference) such will be the outcome.

"Translated into evolutionary terms, this is what competition in nature amounts to. The fluctuating limit of one million to two million represents the finite available wealth (food, shelter, etc.) of any natural environment, and the difference in interest rates represents the difference between the competing species in their efficiency in producing offspring. No matter how small this difference may be, one species will eventually replace the other. In the scale of geological time, even a small competitive difference will result in a rapid extermination of the less successful species. Competitive differences that are so small as to be unmeasurable by direct means will, by virtue of the compound-interest effect, ultimately result in the extinction of one competing species by another."

The Question of Evidence

So much for the theory. Is it true? This sounds like a straightforward question, but it hides subtleties that have, unfortunately, escaped a good many of the ecologists who have done their bit to make the exclusion principle a matter of dispute. There are many who have supposed that the principle is one that can be proved or disproved by empirical facts, among them (*9, 10*) Gause himself. Nothing could be farther from the truth. The "truth" of the principle is and can be established only by theory, not being subject to proof or disproof by facts, as ordinarily understood. Perhaps this statement shocks you. Let me explain.

Suppose you believe the principle is true and set out to prove it empirically. First you find two noninterbreeding species that seem to have the same ecological characteristics. You bring them together in the same geographic location and await developments. What happens? Either one species extinguishes the other, or they coexist. If the former, you say, "The principle is proved." But if the species continue to coexist indefinitely, do you conclude the principle is false? Not at all. You decide there must have been some subtle difference in the ecology of the species that escaped you at first, so you look at the species again to try to see how they differ ecologically, all the while retaining your belief in the exclusion principle. As Gilbert, Reynoldson, and Hobart (*10*) dryly remarked, "There is . . . a danger of a circular process here. . . ."

Indeed there is. Yet the procedure can be justified, both empirically and theoretically. First, empirically. On this point our argument is essentially an acknowledgement of ignorance. When we think of mixing two similar species that have previously lived apart, we realize that it is hardly possible to know enough about species to be able to say, in advance, which one will exclude the other in free competition. Or, as Darwin, at the close of chapter 4 of his *Origin of Species* (*11*) put it: "It is good thus to try in imagination to give any one species an advantage over another. Probably in no single instance should we know what to do. This ought to convince us of our ignorance on the mutual relations of all organic beings: a conviction as necessary, as it is difficult to acquire."

How profound our ignorance of competitive situations is has been made painfully clear by the extended experiments of Thomas Park and his collaborators (*12*). For more than a decade Park has put two species of flour beetles (*Tribolium confusum* and *T. castaneum*) in closed universes under various conditions. In every experiment the competitive exclusion principle is obeyed—one of the species is completely eliminated, *but it is not always the same one*. With certain fixed values for the environmental parameters the experimenters have been unable to control conditions carefully enough to obtain an invariable result. Just how one is to interpret this is by no means clear, but in any case Park's extensive body of data makes patent our immense ignorance of the relations of organisms to each other and to the environment, even under the most carefully controlled conditions.

The theoretical defense for adhering come-hell-or-high-water to the competitive exclusion principle is best shown by apparently changing the subject. Consider Newton's first law: "Every body persists in a state of rest or of uniform motion in a straight line unless compelled by external force to change that state." How would one verify this law, by itself? An observer might (in principle) test Newton's first law by taking up a station out in space somewhere and then looking at all the bodies around him. Would any of the bodies be in a state of rest except (by definition) himself? Probably not. More important, would any of the bodies in motion be moving in a straight line? *Not one.* (We assume that the observer makes errorless measurements.) For the law says, ". . . in a straight line unless compelled by external force to change . . .," and in a world in which another law says that "every body attracts every other body with a force that is inversely proportional to the square of the distance between them . . .," the phrase in the first law that begins with the words *unless compelled* clearly indicates the hypothetical character of the law. So long as there are no sanctuaries from gravitation in space, every body is always "compelled." Our observer would claim that any body at rest or moving in a straight line verified the law; he would likewise claim that bodies moving in not-straight lines verified the law, too. In other words, any attempt to test Newton's first law *by itself* would lead to a circular argument of the sort encountered earlier in considering the exclusion principle.

The point is this: We do not test isolated laws, one by one. What we test is a whole conceptual model (*13*). From the model we make predictions; these we test against empirical data. When we find that a prediction is not verifiable we then set about modifying the model. There is no procedural rule to tell us which element of the model is best abandoned or changed. (The scientific response to the results of the Michelson-Morley experiment was not in any sense *determined*.) Esthetics plays a part in such decisions.

The competitive exclusion principle is one element in a system of ecological thought. We cannot test it directly, by itself. What the whole ecological system is, we do not yet know. One immediate task is to discover the system, to find its elements, to work out their interactions, and to make the system as explicit as possible. (*Complete* explicitness can never be achieved.) The works of Lotka (*14*), Nicholson (*15, 16*), and MacArthur (*17*) are encouraging starts toward the elaboration of such a theoretical system.

The Issue of Eponymy

That the competitive exclusion principle is often called "Gause's principle" is one of the more curious cases of eponymy in science (like calling human oviducts "Fallopian tubes," after a man who was not the first to see them and who misconstrued their significance). The practice was apparently originated by the English ecologists, among whom David Lack has been most influential. Lack made a careful study of *Geospiza* and other genera of finches in the Galápagos Islands, combining observational studies on location with museum work at the California Academy of Sciences. How his ideas of ecological principles matured during the process is evident from a passage in his little classic, *Darwin's Finches* (*18*).

"Snodgrass concluded that the beak differences between the species of *Geospiza* are not of adaptive significance in regard to food. The larger species tend to eat rather larger seeds, but this he considered to be an incidental result of the difference in the size of their beaks. This conclusion was accepted by Gifford (1919), Gulick (1932), Swarth (1934) and formerly by myself (Lack, 1945). Moreover, the discovery . . . that the beak differences serve as recognition marks, provided quite a different reason for their existence, and thus strengthened the view that any associated differences in diet are purely incidental and of no particular importance.

"My views have now completely changed, through appreciating the force of Gause's contention that two species with similar ecology cannot live in the same region (Gause, 1934). This is a simple consequence of natural selection. If two species of birds occur together in the same habitat in the same region, eat the same types of food and have the same other ecological requirements, then they should compete with each other, and since the chance of their being equally well adapted is negligible, one of them should eliminate the other completely. Nevertheless, three species of ground-finch live together in the same habitat on the same Galapagos islands, and this also applies to two species of insectivorous tree-finch. There must be some factor which prevents these species from effectively competing."

Implicit in this passage is a bit of warm and interesting autobiography. It is touching to see how intellectual gratitude led Lack to name the exclusion principle after Gause, calling it, in successive publications, "Gause's contention," "Gause's hypothesis," and "Gause's principle." But the eponymy is scarcely justified. As Gilbert, Reynoldson, and Hobart point out (*10*, p. 312): "Gause . . . draws no general conclusions from his experiments, and moreover, makes no statement which resembles any wording of the hypothesis which has arisen bearing his name." Moreover, in the very publication in which he discussed the principle, Gause acknowledged the priority of Lotka in 1932 (*5*) and Volterra in 1926 (*6*). Gause gave full credit to these men, viewing his own work merely as an empirical testing of their theory—a quite erroneous view, as we have seen. How curious it is that the principle should be named after a man who did not state it clearly, who misapprehended its relation to theory, and who acknowledged the priority of others!

Recently Udvardy (*19*), in an admirably compact note, has pointed out that Joseph Grinnell, in a number of publications, expressed the exclusion principle with considerable clarity. In the earliest passage that Udvardy found, Grinnell, in 1904 (*20*), said: "Every animal tends to increase at a geometric ratio, and is checked only by limit of food supply. It is only by adaptations to different sorts of food, or modes of food getting, that more than one species can occupy the same locality. Two species of approximately the same food habits are not likely to remain long enough evenly balanced in numbers in the same region. One will crowd out the other."

Udvardy quotes from several subsequent publications of Grinnell, from all of which it is quite clear that this well-known naturalist had a much better grasp of the exclusion principle than did Gause. Is this fact, however, a sufficiently good reason for now speaking (as Udvardy recommends) of "Grinnell's axiom?" On the basis of present evidence there seems to be justice in the proposal, but we must remember that the principle has already been referred to, in various publications, as "Gause's principle," the "Volterra-Gause principle," and the "Lotka-Volterra principle." What assurance have we that some diligent scholar will not tomorrow unearth a predecessor of Grinnell? And if this happens, should we then replace Grinnell's name with another's? Or should we, in a fine show of fairness, use all the names? (According to this system, the principle would, at present, be called the Grinnell-Volterra-Lotka-Gause-Lack principle—and, even so, injustice would be done to A. J. Nicholson, who, in his wonderful gold mine of unexploited aphorisms (*15*), wrote: "For the steady state [in the coexistence of two or more species] to exist, each species must possess some advantage over all other species with respect to some one, or group, of the control factors to which it is subject." This is surely a corollary of the exclusion principle.)

In sum, I think we may say that arguments for pinning an eponym on this idea are unsound. But it does need a name of some sort; its lack of one has been one of the reasons (though not the only one) why this basic principle has trickled out of the scientific consciousness after each mention during the last half century. Like Allee *et al.* (*21*) we should wish "to avoid further implementation of the facetious definition of ecology as being that phase of biology primarily abandoned to terminology." But, on the other side, it has been pointed out (*22*): "Not many recorded facts are lost; the bibliographic apparatus of science is fairly equal to the problem of recording melting points, indices of refraction, etc., in such a way that they can be recalled when needed. Ideas, more subtle and more diffusely expressed present a bibliographic problem to which there is no present solution." To solve the bibliographic problem some sort of handle is needed for the idea here discussed; the name "the competitive exclusion principle" is correctly descriptive and will not be made obsolete by future library research.

The Exclusion Principle and Darwin

In our search for early statements of the principle we must not pass by the writings of Charles Darwin, who had so keen an appreciation of the ecological relationships of organisms. I have been unable to find any unambiguous references to the exclusion principle in the "Essays" of 1842 and 1844 (*23*), but in the *Origin* itself there are several passages that deserve recording. All the following passages are quoted from the sixth edition (*11*).

"As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera. We see this in the recent extension over parts of the United States of one species of swallow having caused the decrease of another species. The recent increase of the missel-thrush in parts of Scotland has caused the decrease of the song-thrush. How frequently we hear of one species of rat taking the place of another species under the most different climates! In Russia the small Asiatic cockroach has everywhere driven before it its great congener. In Australia the imported hive-bee is rapidly exterminating the small, stingless native bee. One species of charlock has been known to supplant another species; and so in other cases. We can dimly see why the competition should be most severe between allied forms, which fill nearly the same place in the economy of nature; but probably in no one case could we precisely say why one species has been victorious over another in the great battle of life" (p. 71).

"Owing to the high geometrical rate of increase of all organic beings, each area is already fully stocked with inhabitants; and it follows from this, that as the favored forms increase in number, so, generally, will the less favored decrease and become rare. Rarity, as geology tells us, is the precursor to extinction. We can see that any form which is represented by few individuals will run a good chance of utter extinction, during great fluctuations in the nature or the seasons, or from a temporary increase in the number of its enemies. But we may go further than this; for, as new forms are produced, unless we admit that specific forms can go on indefinitely increasing in number, many old forms must become extinct" (p. 102).

"From these several considerations I think it inevitably follows, that as new species in the course of time are formed through natural selection, others will become rarer and rarer, and finally extinct. The forms which stand in closest competition with those undergoing modification and improvement, will naturally suffer most. And we have seen in the chapter on the Struggle for Existence that 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 the 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. We see the same process of extermination among our domesticated productions, through the selection of improved forms by man. Many curious instances could be given showing how quickly new breeds of cattle, sheep and other animals, and varieties of flowers, take the place of older and inferior kinds. In Yorkshire, it is historically known that the ancient black cattle were displaced by the long-horns, and that these 'were swept away by the short-horns' (I quote the words of an agricultural writer) 'as if by some murderous pestilence' " (p. 103).

"For it should be remembered that the competition will generally be most severe between those forms which are most nearly related to each other in habits, constitution and structure. Hence all the intermediate forms between the earlier and later states, that is between the less and more improved states of the same species, as well as the original parent species itself, will generally tend to become extinct" (p. 114).

Those passages are, we must admit, typically Darwinian; by turn clear, obscure, explicit, cryptic, suggestive, they have in them all the characteristics that litterateurs seek in James Joyce. The complexity of Darwin's work, however, is unintended; it is the result partly of his limitations as an analytical thinker, but in part also it is the consequence of the magnitude, importance, and intrinsic difficulty of the ideas he grappled with. Darwin was not one to impose premature clarity on his writings.

Origins in Economic Theory?

In chapter 3 of *Nature and Man's Fate* I have argued for the correctness of John Maynard Keynes' view that the biological principle of natural selection is just a vast generalization of Ricardian economics. The argument is based on the isomorphism of theoretical systems in the two fields of human thought. Now that we have at last brought the competitive exclusion principle out of the periphery of our vision into focus on the *fovea centralis* it is natural to wonder if this principle, too, originated in economic thought. I think it is possible. At any rate, there is a passage by the French mathematician J. Bertrand (*24*), published in 1883, which shows an appreciation of the exclusion principle as it applies to economic matters. The passage occurs in a review of a book of Cournot, published much earlier, in which Cournot discussed the outcome of a struggle between two merchants engaged in selling identical products to the public. Bertrand says: "Their interest would be to unite or at least to agree on a common price so as to extract from the body of customers the greatest possible receipts. But this solution is avoided by Cournot who supposes that one of the competitors will lower his price in order to attract the buyers to himself, and that the other, trying to regain them, will set his price still lower. The two rivals will cease to pursue this path only when each has nothing more to gain by lowering his price.

"To this argument we make a peremptory objection. Given the hypothesis, no solution is possible: there is no limit to the lowering of the price. Whatever common price might be initially adopted, if one of the competitors were to lower the price unilaterally he would thereby attract the totality of the business to himself. . . ."

This passage clearly antedates Grinnell, Lack, *et al.*, but it comes long after the *Origin of Species*. Are there statements of the principle in the economic literature before Darwin? It would be nice to know. I have run across cryptic references to the work of Simonde de Sismondi (1773–1842) which imply that he had a glimpse of the exclusion principle, but I have not tracked them down. Perhaps some colleague in the history of economics will someday do so. If it is true that Sismondi understood the principle, this fact would add a nice touch to the interweaving of the history of ideas, for this famous Swiss economist was related to Emma Darwin by marriage; he plays a prominent role in the letters published under her name (*25*).

Utility of the Exclusion Principle

"The most important lesson to be learned from evolutionary theory," says Michael Scriven in a brilliant essay recently published (*26*), "is a negative one: the theory shows us what scientific explanations need not do. In particular it shows us that one cannot regard explanations as unsatisfactory when they are not such as to enable the event in question to have been predicted." The theory of evolution is not one with which we can predict exactly the future course of species formation and extinction; rather, the theory "explains" the past. Strangely enough, we take mental satisfaction in this ex post facto explanation. Scriven has done well in showing why we are satisfied.

Much of the theory of ecology fits Scriven's description of evolutionary theory. Told that two formerly separated species are to be introduced into the same environment and asked to predict exactly what will happen, we are generally unable to do so. We can only make certain predictions of this sort: either A will extinguish B, or B will extinguish A; or the two species are (or must become) ecologically different—that is, they must come to occupy different ecological niches. The general rule may be stated in either of two different ways: *Complete competitors cannot coexist*—as was said earlier; or, *Ecological differentiation is the necessary condition for coexistence.*

It takes little imagination to see that the exclusion principle, to date stated explicitly only in ecological literature, has applications in many academic fields of study. I shall now point out some of these, showing how the principle has been used (mostly unconsciously) in the past, and predicting some of its applications in the future.

Economics. The principle unquestionably plays an indispensable role in almost all economic thinking, though it is seldom explicitly stated. Any competitor knows that unrestrained competition will ultimately result in but one victor. If he is confident that he is that one, he may plump for "rugged individualism." If, on the other hand, he has doubts, then he will seek to restrain or restrict competition. He can restrain it by forming a cartel with his competitors, or by maneuvering the passage of "fair trade" laws. (Laboring men achieve a similar end—though the problem is somewhat different—by the formation of unions and the passage of minimum wage laws.) Or he may restrict competition by "ecological differentiation," by putting out a slightly different product (aided by restrictive patent and copyright laws). All this may be regarded as individualistic action.

Society as a whole may take action. The end of unrestricted competition is a monopoly. It is well known that monopoly breeds power which acts to insure and extend the monopoly; the system has "positive feedback" and hence is always a threat to those aspects of society still "outside" the monopoly. For this reason, men may, in the interest of "society" (rather than of themselves as individual competitors), band together to insure continued competition; this they do by passing antimonopoly laws which prevent competition from proceeding to its "naturally" inevitable conclusion. Or "society" may permit monopolies but seek to remove the power element by the "socialization" of the monopoly (expropriation or regulation).

In their actions both as individuals and as groups, men show that they have an implicit understanding of the exclusion principle. But the failure to bring this understanding to the level of consciousness has undoubtedly contributed to the accusations of bad faith ("exploiter of the masses," "profiteer," "nihilist," "communist") that have characterized many of the interchanges between competing groups of society during the last century. F. A. Lange (*27*), thinking only of laboring men, spoke in most fervent terms of the necessity of waging a "struggle against the struggle for existence"—that is, a struggle against the unimpeded working out of the exclusion principle. Groups with interests opposed to those of "labor" are equally passionate about the same cause, though the examples they have in mind are different.

At the present time, one of the great fields of economics in which the application of the exclusion principle is resisted is international competition (nonbellicose). For emotional reasons, most discussion of problems in this field is restricted by the assumption (largely implicit) that Cournot's solution of the *intra*national competition problem is correct and applicable to the *inter*national problem. On the less frequent occasions when it is recognized that Bertrand's, not Cournot's, reasoning is correct, it is assumed that the consequences of the exclusion principle can be indefinitely postponed by a rapid and endless multiplication of "ecological niches" (largely unprotected though they are by copyright and patent). If some of these assumptions prove to be unrealistic, the presently fashionable stance toward tariffs and other restrictions of international competition will have to be modified.

Genetics. The application of the exclusion principle to genetics is direct and undeniable. The system of discrete alleles at the same gene locus competing for existence within a single population of organisms is perfectly isomorphic with the system of different species of organisms competing for existence in the same habitat and ecological niche. The consequences of this have frequently been acknowledged, usually implicitly, at least since J. B. S. Haldane's work of 1924 (*28*). But in this field, also, the consequences have often been denied, explicitly or otherwise, and again for emotional reasons. The denial has most often been coupled with a "denial" (in the psychological sense) of the priority of the inequality axiom. As a result of recent findings in the fields of physiological genetics and population genetics, particularly as concerns blood groups, the applicability of both the inequality axiom and the exclusion principle is rapidly becoming accepted. William C. Boyd has recorded, in a dramatic way (*29*), his escape from the bondage of psychological denial. The emotional restrictions of rational discussion in this field are immense. How "the struggle against the struggle for existence" will be waged in the field of human genetics promises to make the next decade of study one of the most exciting of man's attempts to accept the implications of scientific knowledge.

Ecology. Once one has absorbed the competitive exclusion principle into one's thinking it is curious to note how one of the most popular problems of evolutionary speculation is turned upside down. Probably most people, when first taking in the picture of historical evolution, are astounded at the number of species of plants and animals that have become extinct. From Simpson's gallant "guesstimates" (*30*), it would appear that from 99 to 99.975 percent of all species evolved are now extinct, the larger percentage corresponding to 3999 million species. This seems like a lot. Yet it is even more remarkable that there should live at any one time (for example, the present) as many as a million species, more or less competing with each other. Competition is avoided between some of the species that coexist in time by separation in space. In addition, however, there are many ecologically more or less similar species that coexist. Their continued existence is a thing to wonder at and to study. As Darwin said (*11*, p. 363)—and this is one more bit of evidence that he appreciated the exclusion principle—"We need not marvel at extinction; if we must marvel, let it be at our own presumption in imagining for a moment that we understand the many complex contingencies on which the existence of each species depends."

I think it is not too much to say that in the history of ecology—which in the broadest sense includes the science of economics and the study of population genetics—we stand at the threshold of a renaissance of understanding, a renaissance made possible by the explicit acceptance of the competitive exclusion principle. This principle, like much of the essential theory of evolution, has (I think) long been psychologically denied, as the penetrating study of Morse Peckham (*31*) indicates. The reason for the denial is the usual one: admission of the principle to conciousness is painful. [Evidence for such an assertion is, in the nature of the case, difficult to find, but for a single clear-cut example see the letter by Krogman (*32*).] It is not sadism or masochism that makes us urge that the denial be brought to an end. Rather, it is a love of the reality principle, and recognition that only those truths that are admitted to the conscious mind are available for use in making sense of the world. To assert the truth of the competitive exclusion principle is not to say that nature is and always must be, everywhere, "red in tooth and claw." Rather, it is to point out that *every* instance of apparent coexistence must be accounted for. Out of the study of all such instances will come a fuller knowledge of the many prosthetic devices of coexistence, each with its own costs and its own benefits. On such a foundation we may set about the task of establishing a science of ecological engineering.

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