

Competition, Competitive Repulsion, and Coexistence

(faunal equilibriums/exclusion principle/niche/ecologic range)

P. J. DARLINGTON, JR.

Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138

Contributed by P. J. Darlington, Jr., August 14, 1972

ABSTRACT This manuscript is concerned with concepts rather than abstruse details or mathematics. Discussed are: competition; extended competition, proposed for competition in the strict sense, extended and modified by all related interactions including predation, parasitism, disease, and even cooperation, all of which can be "weapons of competition"; competitive repulsion, proposed for the sum of forces that determine spacings, including ecologic spacings, of individuals and populations; Darwin (biotic) equilibriums; competitive extinction, Gause's principle, limited and limiting resources, and single-resource competition; de facto coexistence of competing species, exemplified by green plants competing for sunlight; niche competition; the two concepts of competitive exclusion; deviation of resources and of their utilizers; cause and effect in real situations; and niches, niche overlap, and coexistence. Stressed is the complexity of the real world, and the confusion that can and does arise from modeling it too simply.

This manuscript is not concerned with abstruse details or mathematics, but is a reassessment of some general ecological and evolutionary concepts. These concepts, including those of competition, repulsion, biotic equilibrium, exclusion, coexistence, and the niche, are under intense study now by both naturalists and mathematical biologists, but are not consistently defined and not yet adequately understood. In order to facilitate understanding among all interested persons, I think it is important to define and discuss these concepts in terms consistent as possible with ordinary usage.

THEORY

Definitions and categories of competition

In ordinary usage "competition" means a contending of rivals for almost anything, either directly by almost any means ("all is fair in love and war") or indirectly (as for resources or markets in commerce). Biologists usually define "competition" more narrowly, as including only actions and interactions (or exploitations and interferences, or "active demand") of individuals or species seeking the same "resources." This definition is intended to be precise but in fact is not, for it leaves open the question of what "resources" are. Food and (for green plants) light clearly are resources that are competed for. Many biologists would say that competition occurs also for such things as mates and territories. But are mates and territories resources? Is a multidimensional "niche" a resource? Is space as such a resource? If so, are places in a biota or simply places on the earth resources?

Biologists usually exclude predation from their definition of competition, and this raises further questions. When a fox kills and eats a rabbit, is this competition, and if not, how is

it related to competition? It can be argued that fox and rabbit compete for the energy the rabbit represents or for the space the rabbit occupies; if there were fewer foxes there would be more rabbits. Predation can have additional, indirect effects. If a predator depends on one species of prey, the prey may survive indefinitely, with only limited population fluctuations. But if the predator utilizes two prey species, one may be reduced to extinction. In this case, one species of prey becomes extinct as a result of the presence of the other. Is this competition? Disease and parasitism can have similar effects; species that tolerate them can eliminate or repel those that do not. Mayr (ref. 1, p. 75), quoting Haldane, calls disease a "weapon of competition." A recent note in *Nature* (2) summarizes an apparent example: tsetse-fly-carried trypanosomes, tolerated by native African big game but fatal to many incoming herbivores (e.g., to cattle brought by man) may protect the African fauna against immigrants from other continents. Is this competition?

Attempts to answer these questions and to fix a precise biological definition of competition do not seem to clarify the subject. Recognition of different categories of competition seems more likely to do so. Of the many categories that might be distinguished, I shall now propose and discuss three: extended competition, single-resource competition, and niche competition.

Extended competition and competitive repulsion

The term *extended competition* is now proposed to include competition, in the strict sense, extended and modified by any and all related processes and interactions, including predation, parasitism, disease, and even cooperation—cooperation is a "weapon of competition" if success of the cooperators reduces the success of competing forms. This totality of interactions is, of course, Darwin's "struggle for existence." It can be considered as "competition for places in the world" and as including "any interaction among (plants and) animals, no matter how complex and indirect it may be, that is or may be disadvantageous to any of them" (ref. 3, p. 23).

A useful, evocative term derived from "extended competition" is *competitive repulsion* (see physicists' "repulsion" among atoms), now proposed for the sum of all forces that determine the spacings (including ecologic spacings), and thus the numbers, both of individuals in populations and of populations everywhere. [I coined this term, then found that E. O. Wilson (ref. 4, p. 195) had already used "repulsion" in a similar but more restricted way, and it may well have been used by other biologists.] Competitive repulsions determine biotic equilibriums. The existence of biotic equilibriums is one

of the fundamental facts of evolution, biogeography, and ecology. It is not a new discovery of mathematicians, but has been recognized since Darwin (ref. 5, p. 109), who said,

. . . as from the high geometrical powers of increase of all organic beings, each area is already fully stocked with inhabitants, it follows that as each selected and favored form increases in number (of individuals), so will the less favored forms decrease But we may go further than this; for as new forms are continually and slowly being produced, unless we believe that the number of (species) goes on perpetually and almost indefinitely increasing, numbers must inevitably become extinct.

This is the first statement of the relation between additions and subtractions of species that produces biotic equilibriums. Because Darwin did state this relation, even though imprecisely, and in order to emphasize the continuity of this and many other concepts from the pre-mathematical era of biology to the present, I propose that the equilibriums that determine numbers of individuals and of species in "each area" be called *Darwin equilibriums*.

Evidences of such equilibriums in time and space, and their relation to competition, have been summarized elsewhere (ref. 3, p. 553), thus:

Throughout the recorded history of (animals), whenever the record is good enough, the world as a whole and each main part of it has been inhabited by . . . fauna(s) that (have) been reasonably constant in size and adaptive structure. Neither the world nor any part of it has been overfull of animals in one epoch and empty in the next, and no great ecological roles have been long unfilled Existing faunas show the same balance. Every continent has a fauna reasonably proportionate to its area and climate, and each main fauna has a reasonable proportion of herbivores, carnivores, etc. This cannot be due to chance. Something holds the size and composition of faunas within limits in spite of continual changes and successions in separate phylogenetic groups. Only (extended) competition can do this, and to do it competition (competitive repulsion) must be a fundamental, ever-present force (maintaining faunal equilibriums).

MacArthur and Wilson (6), and others, have now begun to develop mathematical models for analyzing and predicting biotic equilibriums. However, although the theory can be treated with mathematical precision, the different interactions that determine equilibriums in actual cases cannot yet be sorted out, except in artificially simple situations. We can count the numbers of individuals and of species in biotas, and relate the numbers to area, distance, and other factors, but we cannot yet separate the parts played by competition in the strict sense, predation, and disease, and by cooperation and co-evolution, in determining the numbers. The concepts of extended competition, and of competitive repulsion resulting from a totality of interactions, cover cases like this.

Competitive extinction, Gause's principle, and single-resource competition

The concept of *competitive extinction* too is an old one. Darwin (ref. 5, p. 110) thought that species that "stand in closest competition" will affect each others' numbers, and that some will become extinct. Volterra, Lotka, and Haldane, in the 1920s and 1930s, treated competitive extinction mathematically. Gause (7) was apparently the first to demonstrate it experimentally.

One of Gause's generalizations is often called "Gause's principle," and is often misunderstood. In a summary (p. 113)

Gause said (not in exactly these words) that extinction of one of two competing populations will follow when a resource competed for is completely utilized (he said "completely seized"); and in Gause's model limitation of the resource was the *only* factor limiting growth of the populations. The principle that Gause did in fact expound may reasonably be called *Gause's principle* and may be restated thus: two populations (species) cannot long coexist if they compete for a vital resource limitation of which is the direct and only factor limiting both populations. As thus restated, the principle is, I think, valid without exception.

The relatively simple competition involved in this case may be called *single-resource competition*. It may occur among the most diverse organisms. For example, grass-attacking viruses, grasshoppers, geese, and cattle may compete for grass, and any one of them may cause competitive extinction of any other.

Limited and limiting resources

Resource competition does not always lead to extinction. Two or more species that compete for an essential resource often seem to coexist, and obvious ways can be suggested in which they may do so. For example, two species that depend on the same resource may coexist if their populations are limited by separate density-dependent factors (say, each by its own virus disease) so that the two together do not fully utilize the resource. A case like this is analyzed mathematically and graphically by Wilson and Bossert (ref. 8, chap. 3, p. 161, Fig. 18, case 4). A more complex case (competition for light by diverse plants) is considered below. In these cases, limitation of the resources no longer directly and simply limits the populations, and the cases do not invalidate Gause's principle.

Cases like these emphasize the need to distinguish *limited* from *limiting*, and *directly and simply* from *indirectly and complexly limiting* resources. The world is a limited area; all resources are limited; and all normal populations will increase to the point of utilizing the whole of even the most abundant resource, unless other factors prevent the increase. (Human populations are now facing this fact.) The phrase "limited resource" is therefore redundant. What is important in analyses of competition is to distinguish resources that actually are limiting, and further to distinguish whether limitation of a resource is the direct and only factor limiting populations in a given case. The distinction is really between situations in which the outcome is determined by a single factor and situations in which two or more factors interact.

Confusion resulting from failure to make these distinctions is exemplified by recent controversy in *Nature* about "competitive exclusion" [see refs. 9 and 10, and papers there cited]. The controversy concerns an interesting experiment by Ayala (11, 12) in which populations of two species of *Drosophila* competed in half-pint bottles for fixed amounts of food, and in which competition ended in an equilibrium between the populations rather than in extinction of either one. Ayala argued that this invalidated the "so-called principle of competitive exclusion or Gause's principle." However, the number of individuals in the two coexisting populations together was only $252 + 278 = 530$, although the numbers of either species alone that the same amount of food and space would support were 664 and 1251, respectively. Each population, in effect, set a density-dependent limit on increase of the other before the food was fully utilized.

Of course food and space still were limiting factors in Ayala's experiment. If amounts of food and/or space had been increased, both populations would presumably have increased. But the resources exerted limiting effects indirectly, complexly, and without being fully utilized. Limitation of a resource was not the direct and only factor limiting the populations, and the results do not invalidate Gause's principle. However, the question of "validation" is relatively unimportant. The real importance of Ayala's experiment seems to me to be 2-fold. First, it illustrates the beginning of one path of transition (many others are possible) from single-resource competition toward more complex niche competition (below). Second, it provides a real (not mathematical) model showing that an increase of populations after an increase of a resource is not sufficient proof that limitation of the resource is limiting the populations in a direct and simple way.

De facto coexistence of competitors; niche competition

Coexistence of species competing for a vital resource is conspicuous everywhere around us. The resource is light. Sunlight is a vital resource for green plants, and competition for it is intense. Nevertheless, large numbers of green-plant species coexist. How do they do it?

Sunlight can be divided to some extent, but not indefinitely. There is apparently little adaptive differentiation of photosynthetic pigments among large terrestrial plants; the leaves of most such plants absorb the same wavelengths of light (ref. 13, pp. 11, 17). When, therefore, 375 species of trees reach the canopy in 23 hectares (less than $1/10$ square mile—about $0.25/\text{km}^2$) of tropical rain forest (P. W. Richards, in ref. 14, pp. 149–153), they cannot be supposed to divide the light into hundreds of different fractions, as seed-eating birds might divide seeds into hundreds of fractions according to the sizes and other variable characteristics of the seeds. The plants divide themselves, not the light, into fractions. It is as if the birds could not divide the seeds beyond a certain point, but instead divided themselves into many fractions (populations) differing in size, shape, and behavior of individual birds, but still competing intensely for exactly the same seeds. Actually, the birds in this imaginary case, and the plants in fact, divide *themselves and their environment* into fractions by complex processes of co-evolution. The fractions of the environment are commonly called "niches."

Making and occupying niches involves competition not just for one but often for many resources, e.g., among green plants, for space, water, and minerals, as well as for light, and involves also direct interactions among species and diverse "weapons of competition." The sum of all these processes may be called *niche competition*. It includes single-resource competition but limits and modifies the latter in complex ways; niche competition is itself almost infinitely complex, and the outcome of it is often determined, not by limitation of one resource, but by many interacting factors. It is extended competition in action; and it results in evolution of complex systems of competitive repulsions, which determine the sizes and numbers as well as the details of the niches that competing organisms make and occupy.

Competitive exclusion

This discussion has now reached a point that allows critical analysis of competitive exclusion. Biologists define "com-

petitive exclusion" in two quite different ways. It is sometimes taken to mean that two species competing for a vital resource cannot coexist. The principle then involves single-resource competition, is equivalent to Gause's principle, and is valid to the same extent: when, and only when, limitation of the resource is the direct and only factor limiting the populations of both species. The principle of competitive exclusion is also often taken to mean that species that are "ecologically identical" or that occupy "identical niches" cannot coexist. As thus formulated, the principle involves complex niche competition, and is, I think, "true but trivial" [Ayala (ref. 12, p. 1079)], not worth the emphasis it has received, and is more a toy for mathematicians than a biological reality. Different species usually differ in so many ways, and niches involve so many parameters, that the chances of identity either of species' ecologies or of niches must be very small. If populations of two species are limited by separate density-dependent virus diseases (as in a case suggested above), the two may coexist even if they are otherwise ecologically identical. If species directly affect each other (as apparently in Ayala's experiment), each becomes part of the other's niche, and the niches are no longer identical.

The phrase "competitive exclusion" is also misleading. It suggests a static situation, a fencing out, rather than a process. It overemphasizes extreme and over-simplified cases without clearly relating them to more general cases. The general principle is that, if species overlap ecologically in any way, they will compete and will tend to repel each other. Overlapping populations do exert repulsions, which are generated by multiplication of individuals and transmitted by competition. Very often repulsions between two species limit or change the sizes of the populations or the geographic or ecologic ranges of one or both species, or cause evolutionary divergence ("displacement") without causing extinction. Only in extreme cases do repulsions result in local or complete extinction of populations, i.e., in "exclusion."

In short, the concept of competitive exclusion has confused some biologists because they have not defined it consistently. The concept is in itself misleading. It has fostered pointless controversy about the possibility of coexistence of competitors, when what is needed is explanation of the fact that they do coexist.

Resource-division and utilizer division

A distinction between division of a divisible resource (e.g., seeds varying in size) and division of the utilizers of a resource has been made in preceding pages. This distinction seems essential to understanding of real situations, but has apparently not been made or at least not emphasized before. Both kinds of division do occur, *and either may allow coexistence of competing species*. (In most actual cases, however, resources and utilizers are probably both divided in a complex manner.)

Cause and effect in coexistence

It would seem essential, too, not to confuse cause and effect in interpretation of real situations. When ecologists find a resource divided among coexisting competitors, they assume that the division is a permitting cause (i.e., is necessary for) coexistence. The division, however, may equally well be an effect of coexistence, and of resultant competition and competitive repulsion, which may be expected to push competing species into orderly sequences along "resource spectrums."

Niches, niche overlap, and coexistence

A niche, as I understand it, includes the space(s) an organism occupies, its inorganic environment, and other organisms that affect it (these niche components interact in a complex manner), with emphasis often on the resources the organism utilizes, but does not include the organism itself or its own characteristics or behavior, which are niche-making or niche-limiting rather than part of the niche. This distinction is the same as that between a house and the builder-occupier of the house. How niches are made, how they are related to each other, and how many there are or can be in particular cases are questions not yet satisfactorily answered.

May and MacArthur (15) have recently presented a mathematical model of niche overlap, and have concluded that "in a fluctuating (stochastic) environment, the average food sizes for species adjacent in the resource spectrum must differ by an amount roughly equal to the standard deviation in the food size," and that therefore "there is an effective limit to niche overlap in the real world." However, the model is limited in ways that are likely to be nonobvious to readers, and that severely limit its applicability.

The theoretical-mathematical model is not concerned with complex niches but only with single "one-dimensional resource spectrums," and the model is further restricted by the (unstated) condition that limitation of the resource must be the direct and only factor limiting competing populations. Fluctuating (stochastic) environments are referred to, but only as they may cause fluctuations in the resource, not as they may affect populations in other ways. If other factors do join in limiting the sizes of populations, the model is no longer valid (see discussion of Ayala's experiment, above). Moreover, the theoretical-mathematical model is concerned only with the *relation* between niche size and niche overlap (i.e., with d/w ratios in May's and MacArthur's Fig. 1), and tells nothing about actual distances between niches (i.e., nothing about actual values of d) and nothing about the numbers of species that do or may divide a resource spectrum. Concepts of species packing, degree of difference between species, and numbers of species are continually introduced into the discussion of both the theoretical model and real cases, but the model itself is not concerned with any of these things.

This arbitrarily simplified model should be applied only very cautiously to the real world. *The model does NOT require that real species competing for a vital resource must divide the resource into not-too-widely-overlapping fractions.* In complex real situations, even "complete congruence" in use of a resource is possible both in theory and in fact. Coexistence of diverse green plants competing for sunlight (an undivided resource spectrum of wave-lengths) is one example. Coexistence of diverse desert plants competing for water and of diverse aquatic organisms competing for oxygen are other examples.

Even the real cases of resource division cited by May and MacArthur should be interpreted cautiously. It is not safe to assume that, if the utilizers of a resource are found to be differentiated (e.g., by size or by behavior), the resource must be divided correspondingly; often it is, but it need not be, e.g., again different green plants competing for the same sunlight. And it is not safe to assume that, when competitors do divide a resource, the division is a permitting cause of coexistence; it may equally well be a result. Numbers of species do coexist while competing intensely for indivisible or un-

divided resources such as light or (in certain circumstances) water or oxygen; this fact suggests that species competing for other resources may at first coexist without dividing resource spectrums, and that the resource spectrums may be divided later, as a result of competition and competitive repulsion. Actual histories may often have been complex: initial coexistence of competing species may have resulted in some division of both competitors and resources, which may have permitted coexistence of additional species, which may have resulted in further dividing of the resource, etc.

Situations can be looked at even more broadly than this. The total numbers of species that occur together in floras and faunas are determined by complex Darwin equilibriums, which depend in part on extent of available area, minimum viable sizes of populations, diverse interactions among species, and rates of turnover and evolution. Most faunas include herbivores, carnivores, etc.; and in harmonic faunas, the numbers of species making their livings in different ways are in some sort of proportion to the total number of species in the fauna. So, the number of species competing for a given resource is likely to be determined initially, at least in part, by all the factors that affect the whole fauna, and not simply by competition for the one resource. In the course of time, competition may be expected to result in evolution of additional species in the competing set, as described above. At the same time, species may be expected to increase in number in many other sets. This and other processes and interactions will increase both numbers of species and their degree of specialization, and integration in the fauna as a whole.

Niches and ecologic ranges

The niche concept is useful for many purposes but it can be dangerously misunderstood. Even some biologists write as if they think that species in adjacent niches are isolated from each other and do not compete or "avoid competition." In fact, of course, these species do not escape competition but yield to it and use it; competition has put them in their niches, continuance of competition keeps them there, and competition is the means by which niche-occupiers keep other species out of niches.

What must be understood about niches is that they are not previously existing pigeonholes with boundaries (the concept of niche boundaries is, I think, mathematical rather than biological), but are made and continually modified by the organisms that occupy them. This fact can be emphasized by an analogy. It used to be thought that people were born into divinely predetermined "places," or niches, in society. Now, most of us think that people make their own niches; that, where they do not, the niches they are confined to are made by other people; and that the whole complex social structure that results is flexible and capable of evolving. Similarly, ecologic niches are made by the organisms that occupy them; their limits are largely determined by competing organisms; and the whole complex ecologic structure that results is flexible and capable of evolving both in detail and as a whole.

The nature of niches can be further clarified by considering them as ecologic ranges (I hesitate to call them *ecoranges*) and by comparing them with geographic ranges (see ref. 16, p. 177). A given piece of land, say a continent, has geographic dimensions and is potentially able to support a set of species each of which will have a geographic range. The ranges are areas occupied by populations. They do not exist until the

populations occupy them, and they continually change as the populations change. Attempts have been made to divide continents into idealized (and therefore typological) geographic ranges corresponding to climatic zones or major biomes, but (as a zoogeographer) I know that actual species ranges often do not fit the idealized patterns very well. Similarly, a given piece of land has ecologic dimensions and is potentially able to support a set of species, each of which will have an ecologic range. These ranges are ecologic areas occupied by populations. The ecologic ranges do not exist until the populations occupy them, and they continually change as the populations change. To think of them as "niches" invites (typological) idealization and invites also such confusing concepts as "empty niches," "changing niches," "overlapping niches," and "discontinuous niches."

More broadly, a species' total range may be considered to include interdependent geographic and ecologic components both of which are unstable products of the organism's history, characteristics, and behavior.

CONCLUSIONS

"Competition," "competitive exclusion," "niche," and some related terms (including "diversity" and "organization") are not consistently defined and are often used ambiguously. Biologists cannot and perhaps should not agree on rigid definitions of these terms, but persons who use them should define them in the papers in which they are used, and should make the definitions as nearly as possible consistent with ordinary usage.

Extended competition, competitive repulsion, biotic equilibriums, coexistence (and biotic diversity) are complexly interrelated. The relatively simple concepts and principles concerned must be understood before real situations can be understood, but the simple concepts, such as single-resource competition, exclusion, and niche-differentiation, should be applied to complex real situations very cautiously. Emphasis should be on pressures and processes rather than on avoidances and boundaries.

The present short paper is necessarily extremely oversimplified in many ways. Persons who wish more details or mathematical treatments of some aspects of competition, biotic equilibriums, and biotic diversity should consult appropriate works listed below, some of which (17-21) are not referred to elsewhere in this paper. These works have, of necessity, been selected somewhat arbitrarily, but should give

an entry to other, extensive recent literature on competition and related subjects.

I am indebted to Prof. E. O. Wilson for useful discussion and suggestions.

1. Mayr, E. (1963) *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, Mass.).
2. R. A. C. (1972) *Nature* **235**, 248-249.
3. Darlington, P. J., Jr. (1957) *Zoogeography* (John Wiley & Sons, New York).
4. Wilson, E. O. (1971) in *Man and Beast: Comparative Social Behavior*, eds. Eisenberg, J. F. & Dillon, W. (Smithsonian Inst. Press, Washington), pp. 183-217.
5. Darwin, C. (1859) *On the Origin of Species* (John Murray, London; facsimile ed., Harvard Univ. Press, 1964).
6. MacArthur, R. H. & Wilson, E. O. (1967) *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, N.J.).
7. Gause, G. F. (1934) *The Struggle for Existence* (Hafner, New York; reprinted 1964).
8. Wilson, E. O. & Bossert, W. H. (1971) *A Primer of Population Biology* (Sinauer Associates, Stamford, Conn.).
9. Gilpin, M. E. & Justice, K. E. (1972) *Nature* **236**, 273-274, 299-301.
10. Antonovics, J. & Ford, H. (1972) *Nature* **237**, 406-408.
11. Ayala, F. J. (1969) *Nature* **224**, 1076-1079.
12. Ayala, F. J. (1970) *Nature* **227**, 89-90.
13. Horn, H. S. (1971) *The Adaptive Geometry of Trees* (Princeton Univ. Press, Princeton, N.J.).
14. Lowe-McConnell, R. H. (ed.) (1969) *Speciation in Tropical Environments* (Academic Press, New York).
15. May, R. M. & MacArthur, R. H. (1972) *Proc. Nat. Acad. Sci. USA* **69**, 1109-1113.
16. Darlington, P. J., Jr. (1971) *Bull. Mus. Comp. Zool.* **142**, 129-337.
17. Milne, A. (1961) "Definition[s] of Competition among Animals," in *Mechanisms in Biological Competition*, (ed.) Milthorpe, F. L. Symposium XV, Soc. Experimental Biol. (Cambridge Univ. Press, Cambridge, England), pp. 40-61.
18. Levins, R. (1968) "Toward an Evolutionary Theory of the Niche," in *Evolution and Environment* (ed.) Drake, E. T. (Yale Univ. Press, New Haven), pp. 325-340.
19. Brookhaven Symposium No. 22 (1969) *Diversity and Stability in Ecological Systems* (Clearinghouse for Federal Scientific and Technical Information, Dept. of Commerce, Springfield, Va.).
20. Ayala, F. J. (1970) "Competition, Coexistence, and Evolution" in *Essays in Evolution and Genetics . . .* (eds.) Hecht, M. K. & Steere, W. C. (Appleton-Century-Crofts, New York), pp. 121-158.
21. MacArthur, R. H. (1972) *Geographical Ecology* (Harper & Row, New York).