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COMMUNITY EQUILIBRIA AND STABILITY, AND AN EXTENSION OF THE COMPETITIVE EXCLUSION PRINCIPLE

SIMON A. LEVIN

Department of Mathematics, Center for Applied Mathematics, and Section of Ecology
and Systematics, Cornell University, Ithaca, New York 14850

Beginning with the fundamental work of Volterra (1926), a large amount of the ecological literature has dealt with an elaboration of the concept of niche by means of one or another of the various forms of what is known alternatively as the "Gause hypothesis" (Slobodkin 1961a), "Gause's principle" (Odum 1959), or even "Gause's axiom" (Slobodkin 1961a), depending on how one feels about it. I shall take a middle course in this paper, referring to it as the "Gause principle" or the "competitive exclusion principle" and shall generalize the result to other than purely competitive situations, and ones involving an arbitrary number of species.

1. PRELUDE

Although the result is generally attributed to Gause because of his experimental evidence for it, the theory goes back at least to Grinnell (1904, 1917), and was formally developed by Volterra (1926, 1931), who set the stage for all that was to follow. Considering a situation in which all species are resource-limited, Volterra showed that only one species can survive on a single resource. Later theoretical work by MacArthur and Levins (1964; see also MacArthur and Wilson 1967; Levins 1968) extended this concept to show that, in general, there can be no more species than resources. The same theme was developed independently by Rescigno and Richardson (1965), still with the strong limitation that all species are resource-limited.

As stated earlier, an empirical substantiation of this principle—at least in the case of two species feeding on the same resource—came by way of Gause's experiments on competition between *Paramecium caudatum* and *P. aurelia* (Gause 1934).

In isolated cultures, each protozoan species reached a constant positive equilibrium concentration—64 per cubic centimeter in the case of *P. caudatum,* and 105 per cubic centimeter in the case of *P. aurelia.* However,

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after 16 days in a mixed culture containing both species, only *P. aurelia* survived, having won out in competition with *P. caudatum* for the common resource. Thus the principle became generally known as the ''Gause principle,'' rather than the ''Volterra principle,'' although some writers (e.g., Hutchinson 1953; MacArthur 1958) do refer to it as the ''Volterra-Gause'' principle.

Later work on competition (e.g., Utida 1953; Frank 1957; MacArthur 1958; Slobodkin 1961*b*; Park 1962) and on character displacement (see Brown and Wilson 1956) lent strong evidence for the robustness of the result, by somewhat different approaches to the problem. MacArthur studied five species of warbler which are congeneric and so similar in their ecological preferences as to constitute an apparent threat to the Gause principle. However, he succeeded in showing that the feeding habits of the five species were significantly different from one another, and that the species were thus occupying distinct ecological niches, as predicted by the Gause principle.

Character displacement evidence is somewhat more satisfying than the Gause experiments because it demonstrates that the result of such competition need not be the elimination of one species, but instead adaptive changes in the competing species.

In dealing with situations where resources are not the only factors limiting the populations, one must generalize the original statement of the result. If the resources are not in short supply and other factors become crucial, two species can coexist on the same resource, provided they are being limited by different factors. The rule is then modified to its most familiar form: (1) ''No two species can indefinitely continue to occupy the same ecological niche'' (Slobodkin 1961*a*). The danger in this statement is exemplified by the following further quotation from the same source: (2) ''Operationally, it seems most appropriate to define an ecological niche or ecological space as that space which no two species can continue to occupy for an indefinitely long period of time.''

If one accepts this view, one must decide whether one wishes to make statement (1) first, or statement (2); and in a sense it is not possible to make either until the other has been made. On the other hand, the advantage of this approach is that if one assumes that the set defined in (2) is well-defined, no one can any longer dispute the Gause principle, which becomes a tautology.

To get around this difficulty, one must attempt to form the result in terms of an independent definition of ''niche,'' as in the following discussion from Slobodkin (1961*a*) of the concept of the niche as developed by Hutchinson (1957; see also MacFadyen 1957).

Given a region of physical space in which two species do persist indefinitely at (or close to) a steady state, there exists one or more properties of the environment or species, or of both, that ensures an ecological distinction between the two species, and if one were able to construct the multi-dimensional, fundamental niche of these two species a region would be found in this multi-dimensional space that is part of the fundamental niche of one of the species but not of the other; and similarly, a region would be found

that is part of the fundamental niche of the second species but not of the first. It would further be the case that the physical space in which the two species persist indefinitely at, or near, their steady state, represents a real-world projection of those portions of the fundamental niches of the two species that are not identical. If they seem identical the study is incomplete.

The point Slobodkin makes is that there is no extrinsic definition of niche possible that will make the Gause principle testable. The further and crucial objection to this form of the statement is that the conclusion is often drawn (although it certainly does not follow from the statement) that two species can coexist, provided their ecological niches—regarded as hypervolumes in multidimensional space—overlap in what amounts to a ''sufficiently small'' fraction of each. It is the purpose of this paper to show that this is not true, that there are instead certain dimensions of the hypervolumes of paramount importance. Which dimensions those are is determined by which factors are limiting those species, be those factors resources, predators, or others. Two species cannot coexist unless their limiting factors differ and are independent; this is the only criterion one need examine at a given time and place. That is, it is only necessary to determine whether the species differ in this aspect of the niche. Species which appear to fill different niches may be serious competitors. MacArthur (1958)—in the case where all species are resource-limited—comes close to saying this when he says that the proper statement of the Volterra-Gause principle is that ''species divide up the resources of a community in such a way that each species is limited by a different factor.'' Root (1967) clearly recognizes this point when he refers to the ''core of limiting factors that defines the fundamental niche of a particular species.''

2. DEVELOPMENT OF THE MODEL

Let us consider an ecological community made up of n components in densities[1] $x_1, \ldots, x_n$. These components may or may not represent biological species. Depending on the situation, we might want to allow them to be various segments of species in order to study the effects of community inter-actions on natural selection, or they might be chosen to be collections of species which are acting similarly. Further, among the components, we might wish to include measures of various aspects of the community that do not represent biological populations: concentrations of chemical nutri-ents, of shelter, of available space. These present no special problems.

We similarly consider variables $y_1, \ldots, y_m$ which affect the densities of the components in the community, but are external to the community, in the sense that the values of the variables $y_1, \ldots, y_m$ are not significantly affected by the species $x_1, \ldots, x_n$. Examples of these are climatic variables and the densities of some invading species.

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[1] We shall henceforth use the symbols here introduced both to refer to the components per se and to the densities of those components. No confusion is expected to result.

We therefore assume that the dynamics of the community are described by the following familiar modification of the equations of Lotka (1956):

$$\frac{dx_1}{dt} = x_1 f_1 (x_1, \ldots, x_n; y_1, \ldots, y_m), \ldots,$$

$$\frac{dx_n}{dt} = x_n f_n (x_1, \ldots, x_n; y_1, \ldots, y_m).$$

$$(1)$$

For technical purposes, the functions f_i are assumed to be smooth. Fluctuations in the environment are allowed for by means of the inclusion of the parameters $y_1, \ldots, y_m$, as noted above. Invasions can similarly be dealt with through the y variables.

The function $f_i(x_1, \ldots, x_n; y_1, \ldots, y_m)$ represents the growth rate per individual of the ith component. Anything which influences the function f_i is a factor regulating the ith component of the community, and we accordingly call it a *regulating factor* or a *limiting factor* for that component. That is, a limiting factor for component x_i is any x_j or y_k or combination (linear or nonlinear) of them which influences the function f_i, that is, on which f_i depends.

The first observation that must be made is that limiting factors are only locally defined in phase space (the space of variables $x_1, \ldots, x_n$). That is, it is clear that which factors will be so operating for a given component at a given time is determined by the densities of all components in the community and all parameters at that time. The intricacy of these effects is pointed up beautifully in the work of Paine (1966), discussed below in section 5.

A second point is that the definition specifically allows the limiting factors to be combination factors. If for example, a fine-grained species (MacArthur and Levins 1964) utilizes two resources, R_1 and R_2, with proportionate utilization efficiencies, α_1 and α_2, then the true limiting factor for the species is $\alpha_1 R_1 + \alpha_2 R_2$. Certainly R_1 and R_2 individually meet the qualifications listed above for limiting factors; but since there is clearly only one independent limiting factor, it is preferable to discuss limitation in terms of the single factor $\alpha_1 R_1 + \alpha_2 R_2$, rather than the two factors R_1, R_2.

More generally, for the entire community, we assume that there exists a minimal independent set of limiting factors $z_1 (x_1, \ldots, x_n; y_1, \ldots, y_m)$, $\ldots, z_p (x_1, \ldots, x_n; y_1, \ldots, y_m)$, where p will be $\leq n + m$. By a "minimal independent set," we mean one with the property that, near the point in phase space in which we are interested at any given time, each f_i may be expressed as a function only of these factors, and that no smaller collection of factors would suffice for this purpose. In practice, of course, the exact determination of these functions may be extremely difficult.

As we said that $z_1, \ldots, z_p$ are the limiting factors for the components $x_1, \ldots, x_n$, we say in turn that $x_1, \ldots, x_n$ are limited by $z_1, \ldots, z_p$.

With the introduction of the factors $z_1, \ldots, z_p$, the system (1) may be rewritten

$$\frac{dx_1}{dt} = x_1 f_1 (z_1, \ldots, z_p), \ldots, \frac{dx_n}{dt} = x_n f_n (z_1, \ldots, z_p). \qquad (2)$$

As is natural and usually done (Volterra 1926; Kostitsyn 1937; MacArthur and Levins 1964; Levins 1968; Rescigno and Richardson 1965), we make the assumption that the functions f_i are linear functions of $z_1, \ldots, z_p$. (No similar assumption is made however regarding the nature of the factors $z_1, \ldots, z_p$.) The linearity assumption makes graphic the results we are going to prove. However, such strong assumptions are unnecessary, as will be pointed out in the Appendix. The assumption is equivalent to the statement that each f_i can be written $f_i (z_1, \ldots, z_p) = \alpha_{i1}z_1 + \ldots + \alpha_{ip}z_p + \gamma_i$ for suitable constants $\alpha_{i1}, \ldots, \alpha_{ip}, \gamma_i$.

3. EQUILIBRIA AND STABILITY

For every choice of the parameters $y_1, \ldots, y_m$, the right-hand sides of the equations (2) define n functions of the variables $x_1, \ldots, x_n$. As the parameters $y_1, \ldots, y_m$ change, those functions $f_1, \ldots, f_n$ change, but presumably at much slower rates than the variables $x_1, \ldots, x_n$ themselves. Systems for which this is not valid obviously require a somewhat different analysis, as Hutchinson (1953) has suggested (see also Pimentel 1961).

We then are interested in whether the system can tend to some equilibrium, either constant or dynamic, and to what degree that equilibrium is resistant to slight perturbation. For the purposes of this paper, we require the equilibrium to be constant or cyclic (i.e., corresponding to a point orbit or periodic orbit), but for mathematical purposes, this notion could be generalized somewhat (see Appendix). We shall always be interested in the stability of equilibria for which all $x_i > 0$, since if some $x_i = 0$, we simply revise our original equations, removing x_i as a member of the community (and introducing it as a parameter if invasions by it are likely to affect the stability of the community). Thus the equilibria we are interested in are always bounded, and bounded away from the coordinate planes $x_i = 0$.

When one superimposes the random nature of the environment on the system, one expects to find the system oscillating about the purported equilibrium without ever attaining it, but this does not deny the existence of the equilibrium in the deterministic model.

There are several rather distinct measures of stability to apply to ecological situations, each yielding different information. I mention two, although it is only the second we shall apply, because the first deserves much more attention by ecologists than it has received in connection with the stability of ecological systems.

As pointed out at the beginning of this section, the functions f_i are changing, but on a time scale relative to which the x_i will in general appear

to have already reached equilibrium. Thus, as we view the process on this time scale, we see the x_i in movement from one equilibrium to another, and generally by a smooth transition. Such an equilibrium—that is, one which changes smoothly (continuously) into a nearby equilibrium when the functions f_i are slightly altered—is called *structurally stable*. If, however, the community evolves in this smooth way only up to some point where a radical (discontinuous) change takes place, then the equilibrium when this occurs is structurally unstable. An example of this is when some physiographic factor (e.g., a glacial tongue) is gradually splitting a community. At some point, geographical isolation significant enough to allow speciation will result, and this is the point of structural instability. A similar situation occurs during centrifugal speciation (Brown 1957). For a further discussion of this topic and its relation to biological systems, one is referred to Thom (1969) and Lewontin (1969).

We shall be concerned here with what Lewontin (1969) refers to as "neighborhood stability," and what mathematicians know as "asymptotic orbital stability" (Coddington and Levinson 1955). Given that an equilibrium has been attained (and is varying with the changes in the parameters), is it stable with regard to fluctuations in the values of the x_i variables themselves? Any situation which does not satisfy this type of stability criterion cannot long prevail. In the case of the periodic orbit, this does not require that the perturbed state return to the point from which it was perturbed, but merely to some arbitrarily small neighborhood of the periodic orbit as a whole.

4. THE EXTENDED PRINCIPLE

We now state the major result of this paper:

No stable equilibrium can be attained in an ecological community in which some r components are limited by less than r limiting factors. In particular, no stable equilibrium is possible if some r species are limited by less than r factors.

It is not difficult to prove this result. Suppose, without loss of generality (since we may always relabel the components), that the first r components are limited by less than r factors. Then the functions $f_1, \ldots, f_r$, being linear functions of less than r variables, are linearly related; that is, there exist constants $\beta_1, \ldots, \beta_r$ and δ such that $\beta_1 f_1 + \ldots + \beta_r f_r = \delta$. If one now returns to system (2), one infers at once the relation

$$\beta_1 \frac{1}{x_1} \frac{dx_1}{dt} + \ldots + \beta_r \frac{1}{x_r} \frac{dx_r}{dt} = \delta,$$

which clearly may be integrated to yield $\beta_1 \ln x_1 + \ldots + \beta_r \ln x_r = \delta t +$ constant, i.e., $x_1^{\beta_1} \ldots x_r^{\beta_r} = K e^{\delta t}$.

Such a relationship must be valid for every solution to (2), with only the constant K allowed to vary from solution to solution. Thus, in particular the constant δ may be determined by examining any one solution, for

example the proposed equilibrium. Since that equilibrium is constant or cyclic and has all $x_i > 0$ (see section 3 above), it is clear that $x_1^{\beta_1} \ldots x_r^{\beta_r}$ must stay bounded, and bounded away from zero. We may therefore eliminate the possibilities $\delta > 0$, for which $e^{\delta t}$ would grow without bound as t increased, and $\delta < 0$, for which $e^{\delta t}$ would tend to zero. Hence $\delta = 0$, and so the passage from any initial state to equilibrium (or nonequilibrium!) is confined to one of the surfaces $x_1^{\beta_1} \ldots x_r^{\beta_r} = K$. The proposed stable equilibrium must be confined to one such surface. A slight perturbation from it will in general carry the motion onto a different surface, to which it is thereafter constrained. Thus there can be no asymptotic return to the original equilibrium, which was, thus, not a stable equilibrium.

5. CONCLUDING REMARKS

The experiments of Paine (1966) in the intertidal waters at Mukkaw Bay, Washington showed that the removal of *Pisaster,* the top predator, resulted in the reduction of the number of species in the community from 15 to eight. Presumably, the presence of *Pisaster* had made possible the independent operation of a great many more limiting factors than was possible without *Pisaster*. In its absence, species which no longer had to contend with predation were now able to dominate several resources that could previously be divided among more species. Here then was a clear example of the operation of the extended limiting principle.

It can be shown that in certain situations the instability that occurs due to an insufficient number of limiting factors is related to the existence of numerous possible unstable equilibria in the neighborhood of every equilibrium point. When the number of limiting factors is only one less than the number of components, there will in general exist a one-parameter family of such equilibria; if it is two less, there will exist a two-parameter family. Allowing for a random environment being superimposed on the community, J. Dunn (personal communication) has remarked on the relationship between such a situation and a one- or two-dimensional random walk, particularly with regard to the ergodic properties of such walks. (The ergodic property is not valid for three-dimensional walks [Feller 1957].) The relationship of this phenomenon to apparent cyclicity in the size of animal populations bears further study.

Hutchinson (1964) has made this point in a slightly different way: ''If the two species were almost equally efficient over a wide range of environmental variables, competitive exclusion would be a slow process. Both species then might oscillate in varying numbers, but persist almost indefinitely.''

6. SUMMARY

It is shown in this paper that no stable equilibrium can be attained in an ecological community in which some r of the components are limited by

less than r limiting factors. The limiting factors are thus put forward as those aspects of the niche crucial in the determination of whether species can coexist.

For example, consider the following simple food web:
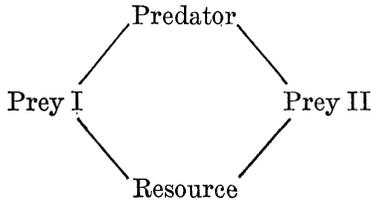
Despite the similar positions occupied by the two prey species in this web, it is possible for them to coexist if each is limited by an independent combination of predation and resource limitation, since then two independent factors are serving to limit two species.

On the other hand, if two species feed on distinct but superabundant food sources, but are limited by the same single predator, they cannot continue to coexist indefinitely. Thus these two species, although apparently filling distinct ecological niches, cannot survive together. In general, each species will increase if the predator becomes scarce, will decrease where it is abundant, and will have a characteristic threshold predator level at which it stabilizes. That species with the higher threshold level will be on the increase when the other is not, and will tend to replace the other in the community. If the two have comparable threshold values, which is certainly possible, any equilibrium reached between the two will be highly variable, and no stable equilibrium situation will result. This is not the same as dismissing this situation as "infinitely unlikely," which is not an acceptable argument in this case. Hutchinson's point of the preceding section vividly illustrates this.

The results of this paper improve on existing results in three ways. First, they eliminate the restriction that all species are resource-limited, a restriction persistent in the literature. Second, the results relate in general to periodic equilibria rather than to constant equilibria. Third, the nature of the proof relates to the crucial question of the behavior of trajectories near the proposed equilibrium, and provides insight into the behavior of the system when there is an insufficient number of limiting factors.

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Finally, this paper cannot close without an exposition of certainly the most elegant form of the niche theorem (section 1) to appear anywhere (unfortunately without proof). The following is taken from Dr. Seuss's epic "On Beyond Zebra" (Geisel 1955).

> And NUH is the letter I use to spell Nutches
> Who live in small caves, known as Nitches, for hutches.
> These Nutches have troubles, the biggest of which is
> The fact there are many more Nutches than Nitches.
> Each Nutch in a Nitch knows that some other Nutch
> Would like to move into his Nitch very much.
> So each Nutch in a Nitch has to watch that small
>   Nitch
> Or Nutches who haven't got Nitches will snitch.

W. L. Brown, Jr., and R. Root were aware of this statement long before the author, but it should indeed have wider currency.

APPENDIX

The purpose of this section is to make clear the mathematical principles underlying the results of this paper.

We shall call a (finite) set A of functions dependent on a set B of functions, if every function in A is expressible in terms of the elements of B. In this paper, we shall simply call the set A dependent if it is dependent on a set B with fewer elements. It is a simple exercise to show that this property is inherited by any (finite) set C which includes A as a subset, since C is dependent on the set D which is formed by adding to B all the elements in C but not in A. Clearly, if B has fewer elements than A, then D has less than C.

Applied to the functions $f_1, \ldots, f_n$ in (2) when some r components are limited by less than r limiting factors, the definitions above simply say that the set $\{f_1, \ldots, f_n\}$ has a dependent subset containing r elements. By the above remarks, this means that the set $\{f_1, \ldots, f_n\}$ itself is dependent. The principal conclusion of the paper may thus be seen to depend only on the statement (subject to the linearity assumptions): if $p < n$, the system (2) has no point or periodic orbits which are strictly positive (that is, for which each x_i is always strictly positive) and asymptotically orbitally stable (section 3).

Because of the positivity assumption, one can take logarithms in system (2), and the theorem is equivalent to the theorem that if $p < n$ the system

$$\frac{dX_1}{dt} = F_1(Z_1, \ldots, Z_p), \ldots, \quad \frac{dX_n}{dt} = F_n(Z_1, \ldots, Z_p)$$

has no asymptotically orbitally stable periodic or point orbits. Here $Z_j(X_1, \ldots, X_n) = z_j(e^{X_1}, \ldots, e^{X_n}), j = 1, \ldots, n$. An analogous proof to that given previously works if the functions F_i are linear, and can be extended to a much wider class of functions F_i. On the other hand, one can alternatively obtain results for either system by making no assumptions on the F_i, but by taking the Z_j to be linear, for one can then simply introduce $Z_1, \ldots, Z_p$ (as new dependent variables. The proof in the general case (that is, with no such assumptions on the F_i or the Z_j) is still not known (except in a slightly modified form for $n = 2$), and of course this means that the truth of the mathematical theorem itself is still an open question.

One other means of extension is possible, and that is by remarking that the mathematical results proved in this paper remain valid if the notion of a stable periodic orbit is replaced by the more general concept of a closed invariant set which is the union of finitely many orbits. This is a nontrivial mathematical point, but hardly worth discussing in detail here.

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