Can There be More Predators Than Prey?

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1. INTRODUCTION

One of the few general “theorems” of ecology is the statement that in a given habitat there can be no more species present than the number of limiting resources. Our aim is to examine several of the versions of this “theorem” present in the literature, to compare them and to consider the underlying assumptions and definitions so as to decide to what ecological situations the theorem is applicable.

Firstly, we present three examples where the bald statement, “There can be no more species than resources” seems false, in order to illustrate the difficulty of deciding how many resources are present. Secondly, we review three versions of the theorem, point out their limitations and relate them to each other.

2. EXAMPLES

A. Two Predators—One Prey

Consider a single prey species with adult and larval forms, and two predator species, one feeding only on adults and the other only on larvae. At time $t$, let

\[ w = \text{density of larval prey}, \]
\[ x = \text{density of adult prey}, \]
\[ y = \text{density of predator on larvae}, \]
\[ z = \text{density of predator on adults}, \]

and suppose $T$, the time spent in the larval state, is constant.

We suppose that the two predator species are limited only by their food, but that the prey species has some other density-dependent regulation. For sim-
plicity, suppose the density dependence operates only on the rate at which adults produce larval offspring, which is taken to be \( f(x) \) per adult. Following Volterra’s (1926) assumptions, the appropriate equations are:

\[
\begin{align*}
\dot{w} &= xf(x) - aw - bwy - x(t - T)f(x(t - T))p(t, y), \\
\dot{x} &= x(t - T)f(x(t - T))p(t, y) - cx - dxz, \\
\dot{y} &= ewy - gy, \\
\dot{z} &= hxz - kx,
\end{align*}
\]

where \( p(t, y) \) is the probability that a larval prey, born at time \( t - T \), survives to become an adult at time \( t \); it will depend on the values \( y(u) \) for \( t - T < u < t \), and an appropriate form is

\[
p(t, y) = \exp \left( - \int_{t-T}^{t} my(u) \, du \right);
\]

\( a, b, c, d, e, g, h, k, m \) are taken to be positive constants.

Stationary values of \( w, x, y, z \) are

\[
\begin{align*}
\bar{w} &= g/e, \\
\bar{x} &= k/h, \\
\bar{y} &= (e/bg)(\bar{x}(1 - p)f(\bar{x}) - a\bar{w}), \text{ and} \\
\bar{z} &= (1/d)(pf(\bar{x}) - c),
\end{align*}
\]

where \( p = \exp(-mT\bar{y}) \). These will be biologically meaningful provided \( \bar{x}(1 - p)f(\bar{x}) > a\bar{w} \) and \( pf(\bar{x}) > c \); in this case, if \( w, x, y, z \) are kept at their stationary values for at least time \( T \), and then a small displacement is introduced by making \( w = \bar{w}(1 + W) \), etc., where \( W, X, Y, Z \) are small, the system can be shown to be stable in the sense that \( W, X, Y, Z \) quickly decrease in absolute value.

Thus two predator species can be maintained by one prey species if they depend on different stages of the life cycle.

B. Two Herbivores—One Plant

The MacArthur–Levins argument might be thought to apply equally well to the number of herbivorous species which can be supported by a given number of plant species. If a herbivore swallows a plant whole, the argument is identical. But consider two herbivores, one feeding on the leaves and one on the roots of the same plant, and suppose

(i) An annual plant has a density, in a particular year, of \( X \) plants per unit area, each plant producing \( W \) seeds.

(ii) The density of the plant is regulated because the probability of a seed growing into a plant next year is a decreasing function of the seed density \( WX \).
(iii) $Y_1$ and $Y_2$ are the densities of a root-eating and leaf-eating herbivore, respectively, each having annual generations.

(iv) For the root-eating herbivore, the reproductive rate is a decreasing function of $Y_1/X$, the number of individuals per plant; a similar assumption holds for the leaf-eater.

(v) Seed production per plant $W$ is a decreasing function of both $Y_1/X$ and $Y_2/X$.

Investigation of such a model shows that for a wide range of appropriate functions a stable equilibrium with plant and both herbivores is reached.

It follows that different parts of the same plant species can serve as sole limiting factors for different herbivorous species. Clearly, the same argument applies to a host species and its parasites.

C. Self-limited Predators

A third apparent counterexample can be found in Kostitzin (1939, p. 128). Kostitzin takes equations of the form

$$\dot{z}_A = z_A(-a + bx - cz_A - dx_B),$$
$$\dot{z}_B = z_B(-e + fx - gz_A - hz_B),$$
$$\dot{x} = x(k - mz_A - nx_B - px),$$

and shows that one prey species can support two predators.

However, these equations imply self-limitation of the predator. This could arise if, for example, a predator required a minimum territory size. In the long run, territory size will be adjusted by natural selection so that it is large enough to contain enough food for the individual or family occupying it. But in the short run, territory size is a second limiting resource, acting independently of the food supply, so this is clearly not a counterexample to the "theorem."

However, in cases $A$ and $B$, we can only preserve the "theorem" if the larval and adult stages of a prey, or the roots and leaves of a plant, are treated as independent resources. The problem then arises: In what circumstances can two measures $x_1$ and $x_2$ be regarded as independent resources? It is clear, from examples $A$ and $B$, that statistical independence of resources $x_1$ and $x_2$ is not required.

What can be said is that if there is a "nice" function $g$, not identically zero but such that $g(x_1, x_2) = 0$, then $x_1$ and $x_2$ are not separate resources. ["Nice," in this context means that the equation $g(u, v) = 0$ defines a curve in phase space.] For suppose that two species $A, B$ have densities $z_A, z_B$ whose derivatives $\dot{z}_A, \dot{z}_B$ are functions of $x_1$ and $x_2$. Then it is clear from Fig. 1, that, for an equilibrium, three curves must pass through a single point, as in the MacArthur–Levins argument (see Section 3A), since arbitrary small changes in the coefficients of the equations could violate this, such an equilibrium is "infinitely
improbable." This depends on the assumption that there are no processes tending to adjust the coefficients so as to ensure coexistence. The coefficients could be altered by natural selection, but there is no selective force favoring coexistence. Thus, for example, a change in one of the competing species enabling it to maintain itself on a lower concentration of resources would be favored by selection, whether or not it led to the extinction of the other species.

Another way of deciding whether two variables $x_1$ and $x_2$ are properly regarded as one resource or two resources can be gained by considering a finite difference formulation of the theorem. Suppose $\Delta t$ is a time interval short enough to ensure that $x_1$ and $x_2$ do not change significantly during the interval. If the predator densities $z_A, z_B$ are limited only by $x_1$ and $x_2$, we can plot the lines $\Delta z_A = 0, \Delta z_B = 0$ in the $(x_1, x_2)$-plane, as shown in Fig. 2. If $x_1$ and $x_2$ are to
be separate resources, no nontrivial relationships \( g(x_1, x_2) = 0 \) can exist. Consider some possible cases:

(i) Two predators feed on the same prey, but by night and day, respectively. If we take \( \Delta t = 24 \text{ hr} \), and \( x_1, x_2 \) as the number of prey during the day and night, if the life-span of the prey is long compared to 24 hr, then \( g(u, v) = u - v \) is such that \( g(x_1, x_2) = 0 \), and so the prey does not constitute two resources.

(ii) Two predators feed on the same prey, but in winter and summer, respectively. Parallel to (i), if the life-span of the prey is long compared to a year, only one resource is present. But suppose the life-span of the prey is of the order of one year or less. Then, if \( x_1 \) and \( x_2 \) are the numbers of prey in winter and summer, respectively, and \( z_A, z_B \) the densities of the corresponding predators, \( x_1 = f_1(x_2, z_B) \) and \( x_2 = f_4(x_1, z_A) \), so, in general, two separate resources will be present.

(iii) Two predators feed on the same prey, one on the ground and one when flying. Then, provided the time spent on a single flight or a single visit to the ground is short compared to the life-span then \( g(u, v) = u - cv \) is such that \( g(x_1, x_2) = 0 \), where \( c \) is the ratio of the time a prey spends on the ground to the time it spends in flight.

These examples should be sufficient to indicate the pitfalls in judging how many resources are present; two resources need not be statistically independent if they are to limit two species, but there must not be a functional relationship which confines the possible states \((x_1, x_2)\) to a one-dimensional subset of the \((x_1, x_2)\)-plane.

3. SOME VERSIONS OF THE THEOREM

A. The MacArthur–Levins Version

MacArthur and Levins (1964) define an individual or species as “fine-grained” for two resources \( x_1 \) and \( x_2 \) if it utilizes the two resources in the proportion in which they occur (for instance, plankton swallowed by a whale). An individual is “coarse-grained” if it discriminates, and selects mainly grains of one of the resources. They demonstrate that, in either case, two resources can support at most two species in stable equilibrium, and generalise to conclude that \( n \) resources can support at most \( n \) species. The argument is restated in expanded form on pp. 94–97 of MacArthur and Wilson (1967), who point out in addition that if a species is fine-grained for two resources, these two resources can support only the one species; Levin’s version of this point is given in Section C.

The argument is quite simple, and is given for two resources. Let the densities
at time \( t \) of the two resources be \( x_1 \) and \( x_2 \), and suppose that three species \( A, B, \) and \( C \) with densities \( z_A, z_B, \) and \( z_C \) are feeding on these resources. Then if \( z_A \) depends only on \( x_1 \) and \( x_2 \), there will be a line (not necessarily straight) in the \((x_1, x_2)\) plane on which \( \dot{z}_A = 0 \), and similarly we have lines \( \dot{z}_B = 0 \) and \( \dot{z}_C = 0 \) (see Fig. 3). For equilibrium it is necessary that \( \dot{z}_A = \dot{z}_B = \dot{z}_C = 0 \), and since (quoting MacArthur and Levins) “it is infinitely improbable that three or more independent lines will pass through the same point,” we cannot simultaneously have \( \dot{z}_A = \dot{z}_B = \dot{z}_C = 0 \), with each of \( z_A, z_B, z_C \) nonzero.

No difficulty arises in extending the argument to \( n \) dimensions, demonstrating that \( n \) resources can support no more than \( n \) species. Note that at no stage is it claimed that \( n \) species can actually be supported by \( n \) resources.

If two resources are fine-grained, then (see Fig. 1) the resources actually available will lie on a line \( g(x_1, x_2) = 0 \); if the resources are taken in a fixed proportion, then this will be the straight line \( x_1 = kx_2 \). Since this line will not meet even two of the three lines \( \dot{z}_A = \dot{z}_B = \dot{z}_C = 0 \) in a single point, at most one species can be present at equilibrium.

B. The Rescigno–Richardson Version

Rescigno and Richardson (1965) prove that “If \( n \) species attempt to establish themselves in a group of niches numbering less than \( n \), then, after a sufficiently long period of time, some must perish.” From the assumptions about “niches,” it is clear that they are referring to what an ecologist would call resources. However, they consider only the effect of resources which are competed for, such as food or space. In a subsequent investigation (Rescigno, 1968) into three competitors in the same environment, the explicit assumption is made that an increase in the numbers of any species leads to a decrease in the growth rate of all species; hence predator–prey interactions are excluded. Since Levin’s (1970) version includes this possibility too, we will pass directly to this.
C. *The Levin Version*

Levin (1970) considers the fate of $n$ species, densities $x_1, \ldots, x_i, \ldots, x_n$, according to equations of the form

$$\dot{x}_i = x_i f_i(x_1, \ldots, x_n, y_1, \ldots, y_m).$$

(1)

In these equations, $y_1, \ldots, y_m$ represent variables such as climate or invading species; they are nonresponsive in the sense that the $y$'s are not functions of the $x$'s.

Levin then introduces new functions, $z_1, \ldots, z_p$, where $p < n + m$. Each $z$ is a function of the $x$'s and $y$'s, and the $z$'s are chosen so as to be a "minimal independent set," in the sense that each $f_i$ can be expressed as a function of the $z$'s. Levin proves that no stationary equilibrium or continuous cycle is possible unless $p \geq n$. Thus the $z$'s are the "limiting factors," and there must be at least as many independent factors as there are species to be regulated.

The reason for introducing the functions $z$ is not easy for the nonmathematical reader to see. But suppose, for example, that whenever $x_1$ or $x_2$ appeared on the right hand side of an equation, they appeared in the form $(x_1 + 4x_2)$, then it would be appropriate to replace $(x_1 + 4x_2)$ by $z_1$, a single limiting factor. It will be appreciated that, like resources in the MacArthur-Levins theorem, the limiting factors $z_1, \ldots, z_p$ do not have to be independent in a statistical sense, but must not be functionally dependent on one another.

Before comparing these two theorems, we will argue that Levin is wrong to introduce the variables $y_1, \ldots, y_m$. Consider first the equations

$$\dot{x}_1 = x_1 f_1(x_1, y),$$

(2)

$$\dot{x}_2 = x_2 f_2(x_1, y),$$

(3)

where $y$ is not a function of $x_1$ or $x_2$ but may, of course, vary with time. Thus (2) can be rewritten

$$\dot{x}_1 = F_1(x_1, t),$$

which, given initial conditions, may be solved as

$$x_1 = g(t).$$

Thus (3) becomes

$$\dot{x}_2 = x_2 F_2(g(t), t),$$

i.e.,

$$\dot{x}_2 = x_2 h(t).$$

Consider the equation

$$\dot{x}_2 = x_2 (h(t) + \epsilon)$$
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which has the solution

\[ x_2 = Ke^{\epsilon t} \exp \left\{ \int h(t) \, dt \right\}. \]  

(4)

In our case, \( \epsilon = 0 \); so, for equilibrium, \( K \exp\{\int h(t) \, dt\} \) must be bounded away from zero or infinity. Hence the introduction of a small nonzero \( \epsilon \), i.e., making a small change in the net reproductive rate of species \( x_2 \), makes the R.H.S. of (6) either diverge to infinity or decrease to zero according as \( \epsilon > 0 \) or \( \epsilon < 0 \). Thus the system (2), (3) is not stable, even though on the Levin’s argument there are two limiting factors \( x_1, y \).

Clearly the argument extends to \( n \) species and to \( m \) \( y \)-factors, if only \( r \) (\( r < n \)) of the \( n \) species appear as limiting factors. For we can obtain solutions of \( r \) of the equations (1) in the form \( x_1 = g_1(t), \ x_2 = g_2(t) \ldots x_r = g_r(t) \), and then have \( n - r \) equations left of the form

\[ \dot{x}_i = x_i h_i(t) \quad [r + 1 \leq i \leq n], \]

which, exactly as above, lead to unstable solutions.

It follows that the variables \( y_1, \ldots, y_m \) are irrelevant in determining how many limiting factors are present, and so any resurrection of the theorem must begin by considering equations of the form

\[ \dot{x}_i = x_i f_i(x_1, \ldots, x_n, t). \]  

(5)

Necessary conditions for (5) to represent a stable equilibrium are:

(i) There is no subset of \( r \) equations in which fewer than \( r \) densities appear as limiting factors [and hence, as a special case, all \( n \) densities must appear in at least one limiting function \( f_i \)].

(ii) It must not be possible to replace the variables \( x_1, \ldots, x_n \) by functions \( z_1, \ldots, z_p \) (\( p < n \)) such that \( f_1, \ldots, f_n \) can be expressed as functions of \( z_1, \ldots, z_p, t \). [See the Appendix of Levin’s (1970) paper for a discussion of the nontrivial mathematical difficulties which arise when the \( f \)’s are not linear.]

What is the ecological interpretation of these requirements? Condition (i) says something about the minimum complexity of stable ecosystems, including the fact that, in any ecosystem with \( n \) species, the density of each species must influence either its own rate of increase or the rate of increase of some other species in the system. This point is hardly surprising.

Condition (ii) appears to be a very general form of Gause’s principle. Thus suppose, as suggested above, that whenever \( x_1 \) and \( x_2 \) appear in a limiting factor, they appear in the form \( (x_1 + 4x_2) \). This states that, considered as limiting factors, one member of one species is ecologically identical to four
members of the other. Another way of looking at this is to say that all species whose increase is influenced by either $x_1$ or $x_2$ are "fine-grained" as far as these two resources are concerned, since they are always taken in the same fixed proportions.

Thus the condition states that if two species are identical in their role as limiting factors, no ecosystem containing both can be stable. There is an obvious similarity to that formulation of Gause's principle which states that if two species have identical requirements they cannot coexist. There is, however, an important difference. Most formulations of Gause's principle suggest that what is important in determining whether two similar species can coexist is what limits them. The present formulation suggests that what matters is the role they play as limiting factors either of themselves or of other species.

This reformulation of Levin's theorem, omitting the variables $y_1 \cdots y_m$, which stand for climatic factors and other variables not influenced by the densities of the species of the ecosystem, is clearly the correct extension of the Rescigno–Richardson theorem. But it is worth pointing out that these necessary conditions for a stable equilibrium are by no means sufficient, as the trivial example $\dot{x}_i = i$ shows.

Finally, what is the relation between Levin's theorem and that of MacArthur and Levins? In Levin's theorem, nothing distinguishes predator from prey. In fact the distinction is as follows. Suppose we have $l$ predators, densities $z_1 \cdots z_l$, and $m$ prey, densities $x_1 \cdots x_m$. Then

(i) in equations for $\dot{z}_i$, the coefficients of the $x$'s are positive, and

(ii) in equations for $\dot{x}_k$, the coefficients of the $z$'s are negative.

The MacArthur–Levins theorem states that in a stable ecosystem, $l \leq m$. According to Levin, all the variables $x_1 \cdots x_m$ and $z_1 \cdots z_l$ must appear as limiting factors. If $l = m$, none of the $x$'s need appear as a limiting factor for any prey, which can be limited by the $l = m$ predators $z_1 \cdots z_l$. But if $l < m$, then the $m$ equations for $x_1 \cdots x_m$ must be limited by at least $(m - l)$ prey.

It follows that if there are more prey species than predators, at least some of the prey species must be either self-limited, or limited by competition with other prey species. If $l < m$, then $l$ predators cannot be the only factors limiting $m$ prey. In the case of two prey and one predator species, this conclusion is obvious. Thus

$$\dot{x}_1 = x_1(a - bx),$$
$$\dot{x}_2 = x_2(c - dx),$$
$$\dot{z} = -e + fx_1 + gx_2$$

cannot lead to a stable equilibrium unless $a/b = c/d$, which, as usual, is "infinitely improbable."
Summary

The theorem that there can be no more species in a habitat than the kinds of resources on which they depend is discussed. It is shown that two predators can be limited by different stages of the life cycle of the same prey species, and that two herbivores can be limited if they depend on different parts of the same plant. This leads to the question, in what circumstances can two measurable quantities, $x_1$ and $x_2$, be regarded as different resources for the purposes of the theorem, and it is shown that if $x_1$ is functionally dependent on $x_2$, so that a knowledge of one value at any time specifies the other, then they are the same resource, but that otherwise they can act as different resources, even if they are highly correlated. It is shown that variables such as climate and invading species, which are not themselves influenced by the densities of the species to be limited, are irrelevant in determining the number of resources or limiting factors present.

References